University of Alberta

COMPETITION AND FACILITATION IN A SUBARCTIC-ALPINE PLANT COMMUNITY

by

MATTHEW G.E. MITCHELL

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ABSTRACT

Plant interactions can range from competition to facilitation. While competition is the most common outcome in most systems, facilitation may be important but hidden by competitive interactions. This study determined the mechanisms and overall effects of plant interactions on plant aboveground biomass, within-season growth, and abundance for two species, *Artemisia norvegica* and *Carex consimilis*, in a subarctic-alpine meadow in the Yukon. Additionally, the effects of local-scale abiotic and biotic factors on interaction outcomes were investigated. While the overall outcome of plant interactions in this system was weakly competitive, simultaneously both competition and facilitation were present. The balance between competition and facilitation was also dependent on abiotic variables and plant characteristics such as size. However, the strength and direction of these interactions were not correlated with the abundance of either focal species.

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CHAPTER 1

GENERAL INTRODUCTION

Plant interactions

Plant interactions can range from competition to facilitation. Competition is the simultaneous demand by two or more plants for limited environmental resources that results in decreased fitness or growth for both individuals. Mechanisms for competition involve the preemption of resources such as light, soil nutrients, or space by plants in physical proximity to one another. The opposite interaction, facilitation, occurs when a plant reduces stress or some other negative factor for surrounding plants, thereby increasing their performance (Callaway *et al*, 2002). The original individual can benefit or be unaltered by this interaction (Brooker & Callaghan, 1998). Mechanisms of facilitation include plants improving the microclimate around them or reducing the apparency of neighbouring plants to herbivores (Callaway *et al*, 2005). This results in individuals producing or retaining greater amounts of tissue, which should lead to greater interception of resources.

Plant interactions can be both *symmetric* and *asymmetric*. With symmetric competition, for example, two competing individuals will have equivalent negative effects on each other. With asymmetric competition there is a clear winner and loser of the interaction (Keddy, 2001). In natural systems, interactions are not limited to pairs of individuals, numerous individuals and species are able to interact. These interactions can range from *diffuse*, where all individuals and species have equal effects, to *monopolistic*, where a single individual or species has an effect on a focal individual (Keddy, 2001).

The competitive ability of an individual or species is also often of interest in ecological studies and can be defined in two main ways. *Competitive effect* is the damage that a species can do to its neighbours, while *competitive response* is the species' ability to withstand the competitive effects of neighbours (Keddy, 2001). Competitive ability can also be proportional or disproportional to plant size. The ability of an individual to intercept underground resources such as nutrients and water is usually proportional to size, while aboveground, larger individuals have a disproportional ability to intercept light.

A description of competition and facilitation can be modified by a discussion of the *importance* and the *intensity* of plant interactions. Intensity refers to the absolute degree that competition or facilitation reduces or increases the performance of a plant relative to a plant without neighbours. Importance is the relative degree to which competition or facilitation decreases or increases a plant's growth rate, metabolism, fecundity, survival or fitness compared to all other factors that can affect these measures of plant performance (Brooker & Callaghan, 1998). This distinction is relevant, as an interaction may be intense while at the same time be of equal or less importance to plant performance when compared to herbivory or disturbance.

In most systems, competition has been shown to be the dominant outcome of plant interactions, although there is substantial variation in the strength of competition (Goldberg & Barton, 1992). Two main hypotheses have been advanced to explain and predict this variation in relation to large-scale environmental gradients. Grime (1977; Campbell & Grime, 1992) predicted that competition should be unimportant in unproductive environments because plant biomass is low and plants will be unable to

deplete resources. Because productivity is usually directly related to stress, this theory has also been applied to gradients of stress associated with resource availability and herbivory. With low resources or high herbivory, competition should be less intense as there is decreased plant biomass and the ability of plants to deplete resources and prevent their neighbours from accessing these resources is decreased (Bonser & Reader, 1995). In addition, the importance of competition should also decrease as herbivory increases (Gurevitch *et al*, 2000; Olofsson *et al*, 2002). An alternate theory (Tilman, 1988 & 1990; Taylor *et al*, 1990) is that competition strength is constant across productivity/stress gradients but that the resources in question change. This theory predicts that with low productivity, competition should be for belowground resources such as nutrients and water, while at high productivity competition for light should be most important. Predictions of both hypotheses have been extensively tested, yet results have been variable and no clear consensus has been reached (Reader *et al*, 1994; Brooker & Callaghan, 1998). There have also been attempts to reconcile these two theories. Brooker and Callaghan (1998) predicted that while the *intensity* of competition will remain constant over gradients of stress the *importance* of these interactions will decrease. At high levels of stress two plants can compete intensely for resources (Olofsson *et al*, 1999), but their growth will still be largely determined by the levels of abiotic disturbance (Weldon & Slauson, 1986).

While competition is usually the outcome of plant interactions in most systems, facilitation can also be important. Because most studies observe the overall outcome of plant interactions, facilitation can be masked by stronger competitive interactions (Brooker & Callaghan, 1998; Olofsson *et al*, 1999; Pugnaire & Luque, 2001; Bruno *et al*,

2003). In recent years the importance of facilitation has received significant attention. The focus for facilitation has mainly been on "stressful" systems, perhaps due to the influence of Grime's theory on thoughts about plant interactions. This has included arctic and alpine systems (Choler *et al*, 2001) as well as saline marshes and deserts (Bertness & Callaway, 1995; Fowler, 1986).

Alpine and arctic ecosystems are those above the elevational or latitudinal treeline, respectively. These systems are generally characterized by low resource availability, harsh abiotic conditions, short growing season lengths, and small-statured plants (Chapin, 1987; Korner, 2003). Because of this, plant biomass is generally low, and according to Grime's theory competition intensity should be weak. A few studies have investigated the relationship between stress and competition in these systems and in most cases indicate that facilitation is more important as stress becomes more acute (Choler *et al*, 2001; Callaway *et al*, 2002).

More specific relationships between abiotic and biotic variables and the balance between competition and facilitation have rarely been investigated (Pugnaire & Luque, 2001). Choler *et al* (2001) investigated plant interactions along elevational and topographical gradients using five clonal alpine species with a neighbour removal design. They found that interactions changed from competition in low sheltered sites to facilitative in high unsheltered sites. Callaway *et al* (2002) found similar trends. In a study over multiple continents and species, neighbours had negative effects at low sites and positive at high sites. Olofsson *et al* (1999) recorded negative to neutral effects of neighbours on *Ranunculus glacialis* and *Oxyria digyna* individuals in Norway, but did not specifically look at the abiotic and biotic conditions.

Rapid climate change should also be a consideration when working in alpine and arctic systems. Arctic systems in western Canada have undergone temperature increases of 3-4°C in the last 50 years, and precipitation increases of 8% over the last 100 years, with equal or greater increases predicted for the next century (ACIA, 2004). Alpine areas should experience similar temperature increases as well as increased growing season length and nitrogen availability (Korner, 2003). Specifically, the St. Elias Mountains area of Alaska and the Yukon where this study took place, are predicted to experience much greater climate change than surrounding areas, especially increases in precipitation (ACIA, 2004). These changes are small relative to the daily and seasonal fluctuation that alpine plants experience, yet these long-term and persistent changes can still have substantial effects. While this study did not specifically address the impacts of climate change on plant interactions, I experimentally manipulated precipitation with climate change in mind (Chapter 2). Climate change is therefore relevant to this study and must be taken into account when making predictions about how the plant community may change in the future.

Study system & species

This study was conducted in subarctic-alpine meadows of the Ruby Range mountains (61°13'N, 138°16'W, elevation 1750m) of the southwest Yukon Territory, Canada (Fig. 1-1). The site is approximately 600m above treeline and consists of boulderfields (talus) surrounded by continuous alpine tundra vegetation (Fig. 1-2b). Over one hundred plant species have been identified in the region (Tait, 2002), with the

dominant species including *Dryas octopetala* L., *Salix polaris* Wahlenb., *S. reticulata* L. and *Carex consimilis* Holm (McIntire, 1999).

The main herbivores in this system are mammalian and include collared pikas (*Ochotona collaris*: Lagomorpha) (Fig. 1-2a), hoary marmots (*Marmota caligata*: Rodentia), and arctic groundsquirrels (*Spermophilus parryii*: Rodentia). Invertebrate herbivores appear to be rarer, although belowground herbivory has not been investigated in this system. Several factors, particularly predation risk (e.g. Morrison *et al*, 2004), constrain pika foraging to meadows directly adjacent to the blockfield/talus patches on which they live (Fig. 1-2b). Plants within two meters are consistently grazed each year, with plants more than six meters from talus very rarely grazed (McIntire & Hik, 2002 & 2005). This pattern of foraging creates a strong, long-term grazing gradient.

To investigate plant interactions in this system, I chose two common species that represent two of the common growth forms (forb and graminoid) and that are important forage plants for pikas.

Artemisia norvegica Fries. (Asteraceae) is a small perennial, rhizomatous herb with a cespitose growth form. The genus *Artemisia* comprises over 180 species that range from herbs to shrubs and are known for their volatile oils. *A. norvegica* is found through Eurasia and in North America occurs from Alaska south through the Yukon and Alberta to California and Colorado. Preferred habitat for this species includes moist alpine meadows and tundra, rocky slopes, and heathlands (Cody, 2000).

Carex consimilis Holm. (Cyperaceae) is a clonal sedge with rhizomatous growth and an Amphi-Beringian distribution that is restricted in North America to Alaska, the Yukon, and the northwestern part of the Mackenzie District (Cody, 2000). It is part of

the *Carex bigelowii* complex (Brooker *et al*, 2001). Porsild and Cody (1980) consider *Carex bigelowii* to be an arctic, amphi-Atlantic species, which is replaced in the west by the amphi-Beringian *Carex lugens* Holm and *Carex consimilis* Holm. Aiken *et al* (1999) place *Carex consimilis* as equivalent to *Carex bigelowii* subsp. *bigelowii* with *Carex lugens* specified as *Carex bigelowii* subsp. *lugens* (Holm) Egorova.

Study objectives

In this study I attempted to determine the mechanisms and overall effects of plant interactions on plant aboveground biomass and within-season growth for the two focal species. Additionally, I wanted to determine the effect increased resources and grazing history had on these interactions, as well as the effects of local-scale abiotic and biotic factors.

My first objective was to determine the effects that neighbouring plants, both grazing history and current season grazing, and increased precipitation have on the outcome of plant interactions (Chapter 2). I used an experimental approach combining these factors in a factorial design, along with a neighbour removal approach to determine the effect of neighbouring plants on focal individuals. Grazing history was included using the natural grazing gradient while plants were handwatered to simulate increased precipitation. I measured the response of plants to these treatments using leaf demographic measures such as leaf births and deaths over two growing seasons as well as aboveground biomass measures at the end of the experiment. To determine the possible mechanisms for these interactions I measured soil nutrient availability and recorded the grazing status of each plant during the second growing season of the experiment.

My second objective was to determine the important biotic and abiotic controls on the outcome of plant interactions in this system (Chapter 3). I recorded relationships between local scale factors including soil depth, soil nutrient availability, snowmelt date, vegetation cover, grazing pressure, and aboveground standing crop with the outcome and direction of plant interactions. Additionally, I attempted to determine the importance of these interactions relative to the abiotic and biotic conditions with respect to the abundance of the two focal species, as competition and facilitation are assumed to be important for plant fitness and population dynamics.

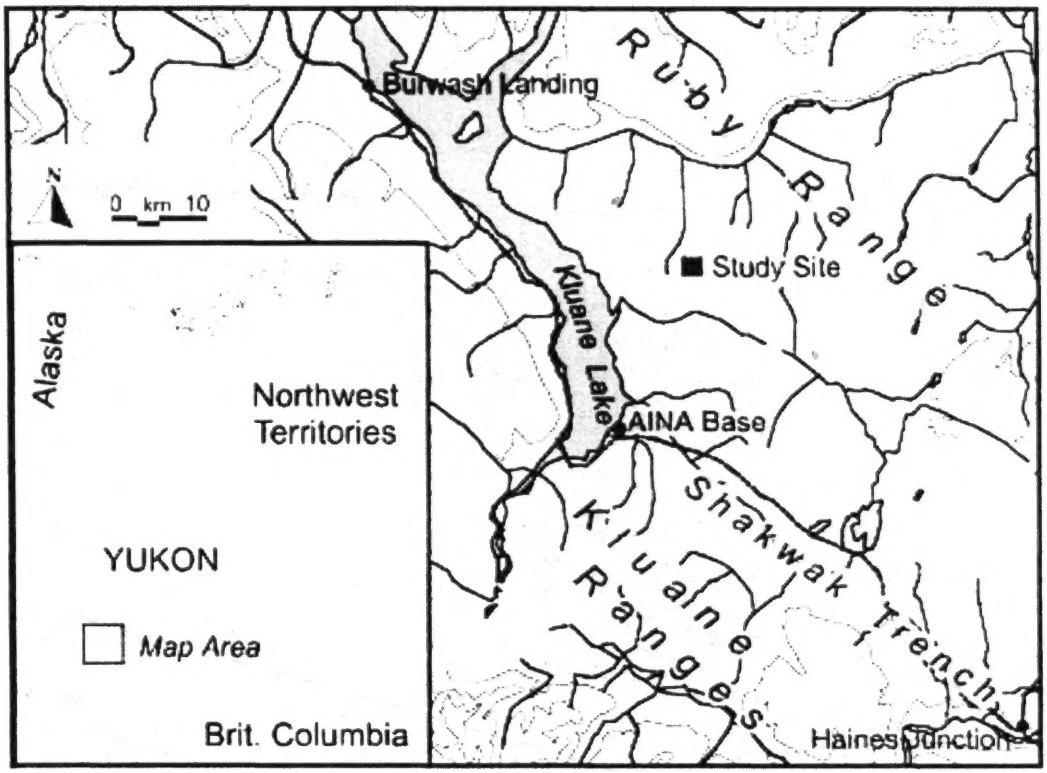

Fig. 1-1 – Maps showing the location of the study site in the southwest of the Yukon Territory, Canada.

A

B

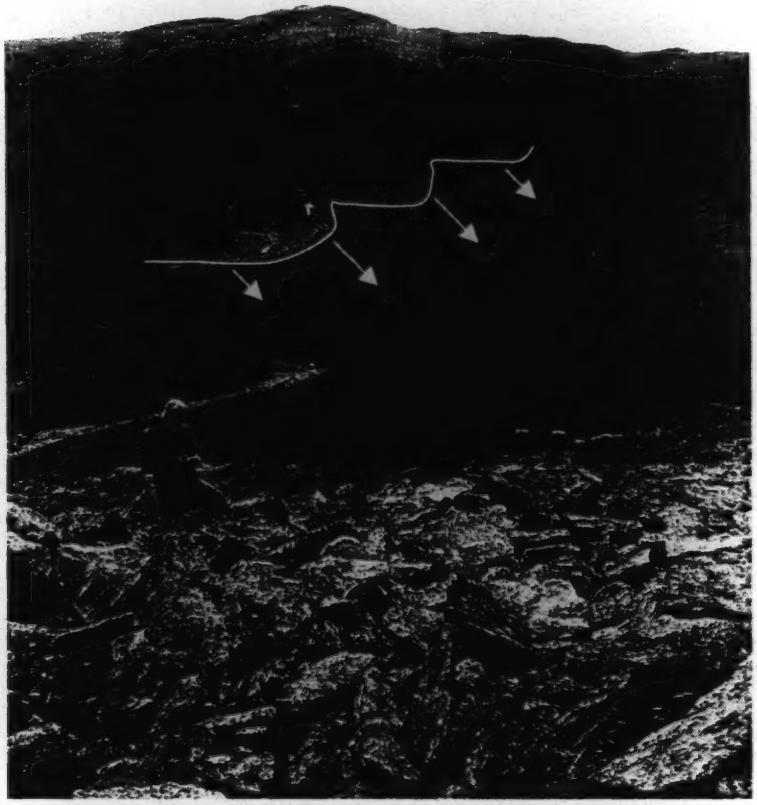

Fig 1-2 – (A) One of the main mammalian herbivores of the system, *Ochotona collaris*. Photo credit: M. Mitchell. (B) The grazing history gradient. Herbivores live mainly in boulderfields (talus) such as that pictured in the foreground. Herbivores graze outward from the margins of these talus patches such that plants near these margins are consistently grazed between years while those farther away are very rarely grazed. A large talus patch is pictured in the background with the margin denoted by a white line. The grazing history gradient follows the arrows moving away from the talus. Photo credit: S. Morrison.

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CHAPTER 2

COMPETITIVE AND FACILITATIVE NEIGHBOUR EFFECTS ON PLANT GROWTH IN A SUBARCTIC-ALPINE PLANT COMMUNITY

INTRODUCTION

Plants are influenced by many extrinsic factors, including competition, facilitation, herbivory, physical stress, and biotic and abiotic disturbance (Grime, 1977; Oksanen *et al*, 1981). In terrestrial systems, competition and herbivory usually have the greatest effect on plant growth and community composition (Maron, 1997; Gurevitch *et al*, 2000; del Val & Crawley, 2005). However, competition and herbivory are expected to have complex interactions in their combined effects on plant growth (Herms & Mattson, 1992; Weis & Hochberg, 2000; Grover, 2002; Haag *et al*, 2004), especially as nutrient availability changes (Taylor *et al*, 1997; Dormann *et al*, 2000).

By limiting a plant's access to resources, competition can alter plant biomass allocation to different tissues (Agrawal & Van Zandt, 2003), change the nutrient or chemical status of the plant (Steinger & Muller-Scharer, 1992; Gerdol *et al*, 2002), or affect its ability to respond to grazing events (Mabry & Wayne, 1997; Damhoureyeh & Hartnett, 2002; Fay & Throop, 2005). In turn, these changes themselves can directly affect a plant's chance of being grazed, or affect the amount of tissue that herbivores will consume. Loss of tissue or a shift in growth due to herbivory has the ability to significantly change the competitive ability or response of a plant (Rodriguez & Brown; 1998; Weis & Hochberg, 2000).

Any factor that affects plant size should also be expected to affect responses to competition and herbivory, although for some species these consequences might not be as important (Gerry & Wilson, 1995; Cahill, 2003). Plant size could mediate these interactions because competitive ability (Horvitz & Schemske, 2002), the ability to respond to herbivory with stored resources, and the chance of being grazed varies with plant size (Pfeiffer & Hartnett, 1995; Osem *et al*, 2004).

Neighbouring plants can improve local abiotic conditions (Korner, 2003; Choler, 2001; Callaway, 2002) and simultaneously decrease resource availability (Pugnaire & Luque, 2001; Rand, 2004), such that positive effects of neighbours make relationships between competition and herbivory even more complicated. The chance of a plant being grazed can also depend on the characteristics of surrounding plants (Atsatt & O'Dowd, 1976; Brown & Ewel, 1987). The palatability of neighbouring plants can alter herbivore behaviour, (McNaughton, 1978; Callaway *et al*, 2005) and neighbours may make individual plants less obvious to herbivores (Rauscher, 1981; Brown & Ewel, 1987; Hamback *et al*, 2000).

Few studies have considered the effects of long-term grazing history on plant characteristics, and these have been limited to plant compensation (Turner *et al*, 1993; Gadd *et al*, 2001) or grazing tolerance (McIntire & Hik, 2002; Adler *et al*, 2004). It has been documented that plant populations respond to various selection pressures, such as grazing (Jaramillo & Detling, 1988; Tomas *et al*, 2000), and that long-lived clonal plants can alter their biomass allocation and physiology in response to environmental factors (Suzuki & Stuefer, 1999; McIntire & Hik, 2002). What is not well understood are the potential impacts long-term grazing history might have on plant-plant interactions. While

chronic grazing might select for specific species or individuals better able to tolerate grazing, there may be traits specific to grazing tolerance or competitive ability that are mutually exclusive, such that there is a negative correlation or trade-off between the two abilities. Also, plants suppressed by chronic grazing may be less able to initiate growth and respond to change (Archer & Tieszen, 1983; Ferraro & Oesterheld, 2002).

For two common alpine species (a sedge and a herb) we investigated the effects and interactions between neighbour removal, watering (to alleviate abiotic stress), and current season and chronic grazing history on plant biomass and leaf demography. We predicted that (1) watered plants with neighbours removed located far from talus would show the largest increases in biomass and growth, because competition should be stronger where grazing has been historically low, due to increased plant biomass and increased abilities to preempt resources from neighbours, and where an abiotic stress has been reduced, (2) high levels of chronic grazing would limit plant growth responses due to long-term suppression of these plants by herbivores, and (3) larger plants would be better able to respond to both negative and positive environmental change during the study.

METHODS

Study area and focal species

This study was conducted in a subarctic-alpine meadow in the Ruby Range mountains (61°13'N, 138°16'W, elevation 1750m) of the southwest Yukon Territory, Canada. The snow-free growing season generally extends from mid-June to late August.

For 1995-2000 mean winter temperatures were -12°C (Oct. – April), and mean summer temperatures were 11°C (June – Aug.), with a mean annual precipitation of 250mm (D. Hik, unpublished data).

The study area consists of a matrix of meadows that surround isolated rock boulder fields. These patches are formed by frost weathering of the bedrock and are generally known as block fields or felsenmeers (Washburn, 1979) but will be referred to as talus patches in this paper. The plant community is dominated by hybrid willow shrubs (*Salix* spp.), sedges (predominantly *Carex consimilis* Holm), *Dryas octopetala* L., *Cassiope tetragona* (L.) D. Don, and various perennial herbs.

The main herbivores present are small mammals, including hoary marmots (*Marmota caligata*: Rodentia), collared pikas (*Ochotona collaris*: Lagomorpha), and arctic ground squirrels (*Spermophilus parryii*: Rodentia). Aboveground invertebrate herbivory is rare (Hik *et al*, 2003), especially for the two focal species of the study (M. Mitchell, pers. obs.), however belowground herbivory has not been quantified for this system. Pikas are small, rock-dwelling, generalist, central-place foraging herbivores of alpine areas (Broadbooks, 1965). As central-place foragers they nest within the talus patches and graze mainly within 6m of the margin of the talus, with plants inside 2m of the talus margins consistently grazed from year to year (McIntire & Hik, 2002 & 2005; Morrison *et al*, 2004). This has created a strong, long-term herbivory gradient with respect to distance from talus. Thus, this system provides a suitable location to investigate the effects of long-term/chronic (grazing history) and short term (current season) grazing on plant growth responses.

Two common species with different growth forms were chosen for this study. *Artemisia norvegica* Fries. (Asteraceae) is a small perennial, rhizomatous herb with a cespitose growth form and apical meristems. *Carex consimilis* Holm. (Cyperaceae) is the dominant sedge in the community (Cody, 2000). We will refer to each species by its genus name below. Both species are used extensively by mammalian herbivores, exhibit extensive clonal growth and were present in sufficient numbers throughout the study area and along the grazing gradient to allow individuals to be identified within reasonably sized plots. These two species should also respond to abiotic and biotic changes within two seasons, and more quickly than woody species.

Experimental design

Two levels each of grazing history (i.e. distance from talus), watering, and neighbour removal were applied to individuals of both focal species over two growing seasons (2003 & 2004) in a split-split block layout. Plot setup and treatment application occurred over two weeks from June 26 to July 8, 2003. Fifteen blocks were located on an east-facing slope that contained several large talus patches with well-defined margins. A single slope was used to minimize interference with other long-term experiments.

Each block consisted of two 2m x 20m plots oriented parallel to a nearby talus patch (Fig. 2-1). One plot was located within 2m of the talus patch margin (evaluated as the boundary where the predominant substrate switches from boulders to soil). The second plot was located 8m away from the first plot. These two distances incorporated the two levels of the grazing history treatment such that plants in the near-to-talus plot had

experienced higher levels of historical grazing relative to those plants in the far from talus plot.

Each distance from talus plot was split into two 2m x 10m subplots into which the two levels of the watering treatment were assigned. Each plot was oriented perpendicular to the main slope, therefore only plants in the lower subplots were watered to minimize any effect of water throughflow. The watering treatment involved supplemental watering, with plants receiving either an approximate 50% increase in growing season precipitation or no extra water (i.e. ambient precipitation). Normal growing season precipitation is ~180mm (D. Hik, unpublished data) so plants received ~90mm extra precipitation during each growing season. This is a relatively large increase, but should be consistent with the interannual variability between wet and dry years for this system. Watering was performed by hand-watering individuals with 500ml of water every 3 days (equivalent to 8mm of precipitation over the 0.25m x 0.25m competition plot; see below). If a significant rainfall event (i.e. > 10mm) occurred within 24 hours of a scheduled watering then watering was cancelled as the soil was saturated. In 2003 the watering treatment began on July 14 and plants received a total of 4.5l (72mm total), while in 2004 watering began on June 18 and 6.5l of water was provided (104mm total). This resulted in an addition of 11 liters total, or 176mm of precipitation over the two growing seasons.

Each subplot was divided into twenty 1m x 1m squares. Only the top and bottom sixteen squares were used in each subplot (Fig. 2-1), with the remaining eight squares retained as a buffer between watering treatments or used when focal plants could not be found in the initial sixteen squares. Each square was randomly assigned a focal species (*Carex* or *Artemisia*) and the individual of that species closest to the middle of the square

was chosen. This resulted in eight individuals of each species within each subplot of which half were assigned to each of the two levels of the competition treatment. The competition treatment consisted of either neighbour retention or removal. For neighbour removal, all aboveground neighbour biomass within a 0.25m x 0.25m square around the focal individual was removed by clipping. Roots were severed to a depth of 10cm along the same boundary. Mosses and lichens were left intact to minimize soil disturbance and exposure. This treatment was maintained throughout the study (regrowth reclipped and roots severed three times in both 2003 and 2004).

This design resulted in a total of 480 individuals of each species: 60 individuals total of each species in each of the eight treatment combinations (within a block, four individuals of each species in each of the eight treatment combinations).

Variables measured

Initial plant size was recorded as the number of live leaves on each plant at the beginning of the first growing season. Subsequently, leaf demographic variables were recorded for each individual every two weeks for both growing seasons in order to provide a measure of the growth and plasticity of individual plants. Measurements included the number of live leaves, leaf births and deaths, and grazed leaves over the previous two-week period. Grazed leaves were identified as those with obvious mammalian herbivore damage: complete removal of the leaf for *Artemisia*, and loss of a significant apical portion of the leaf for *Carex*. There were three sampling dates in 2003 and four in 2004.

At the end of the growing season in 2004 all aboveground biomass of focal individuals was collected. Due to the nature of the alpine soils, the dense roots, and the clonal growth form of the species, it was not feasible to collect roots. The aboveground plant material was sorted into live and dead leaves, and dried to constant weight at 70°C for a minimum of 3 days and weighed to 0.0001g. To investigate neighbour effects on plant nutrient status, a subsample of 30 individuals of each treatment combination (240 individuals total) was also analysed for carbon and nitrogen content using the Dumas dry-combustion technique on a Carlo-Erba 1500 NC analyzer (Strada Rivol Tana; Milan, Italy).

To examine abiotic differences along the grazing history gradient (i.e. distance to talus) as well as the effects of neighbour removal and watering, a variety of abiotic variables were measured over the course of the study. Soil nitrogen availability was determined by using ion exchange resin bags, a method that simulates nutrient uptake by plant roots (Qian & Schoenau, 2002) and allows qualitative analysis of nitrate and ammonium ion availability. Eight grams of DOWEX MR-3 mixed bed ion exchange resin (Aldrich Chemical Company; Milwaukee, WI.) was placed in nylon bags and prepared according to the methodology described by Thiffault *et al* (2000). Single bags were placed in plots of each treatment combination in each block (240 bags total - 30 in each treatment combination) 10cm beneath the soil surface for six weeks during the 2004 growing season. A large number (84 near to talus; 53 far from talus) of the bags were lost to marmots over the summer. Remaining bags were removed on August 8th and were air dried before transportation to the laboratory. Ions captured by the resin were extracted by agitating the resin in 100ml of a 2N NaCl solution for 90 minutes, and the

subsequent solution analysed for nitrate and ammonium ion concentration with a Dionex 600 Ion Chromatograph (Dionex Corporation; Sunnyvale, CA) and a Technicon Autoanalyzer II (Technicon Industrial Systems; Tarrytown, NY), respectively.

Snowmelt date was determined by placing small iButton temperature dataloggers (Maxim Integrated Products; Sunnyvale, CA) in the plots just below the moss layer at the end of the growing season of 2003. Dataloggers were recovered at the beginning of the growing season in 2004 and snowmelt date was determined where large diurnal fluctuations in temperature appeared. Soil depth was determined at four places in each subplot (1, 3, 5, and 7m from the outside end) by sliding a thin metal probe into the soil in three places 5cm apart. We also measured soil moisture content in watered and unwatered plots. Soil samples 2cm x 2cm x 2cm in dimension at a depth of 10cm were collected from plots of each treatment combination in seven blocks, five times over the 2004 growing season. These samples were immediately weighed to determine wet weight and were then subsequently weighed after drying at 100°C for three days to constant weight. Values of the five samples were averaged and water content of the soil presented as percent content by weight because of the difficulty of collecting a consistent soil volume due to the peaty and mossy nature of the soils in this system.

Plant size

We used the initial number of live leaves present on individual plants as a metric of plant size. To determine the strength of this metric we examined relationships between leaf number and biomass of *Artemisia* for 75 individuals collected both adjacent to talus and 10m from talus in the summer of 2005. Leaf number was recorded and

leaves and underground rhizomes were collected. Plant parts were dried to constant weight for 3 days at 70°C and then weighed to 0.0001g. Relationships between leaf number and above- and belowground mass were determined with least squared means linear regression in SPSS 11.0.4 for Macintosh OS X (SPSS Inc., 2005).

Data analysis

Data were analysed using general linear mixed models (GLMMs) in SAS 8.02 (SAS Institute, 2001) using the Proc MIXED statement. Analysis of fixed effects was conducted using Type III sums of squares and the Satterthwaite method for estimating degrees of freedom. Random effects included in the models included Block plus all levels of interactions of Block with the fixed effects. Random effects and interactions were removed from the model if shown to be non-significant. This was done by sequentially removing the random factor or random interaction with the lowest covariance parameter estimate from the model and comparing the –2 Log Likelihood value of the simplified model with that of the full model (Milliken *et al*, 1996). When the difference between the two Log Likelihood values is greater than the critical value of a Chi-Squared test with 1 degree of freedom (i.e. 2.6), then the simplified model is significantly different than the full model and should not be used. Removing these interactions from the model allows the analysis to increase the denominator degrees of freedom for fixed effects and increase the power of the ANOVA to detect differences. Block was never removed from the analysis, as it was structural to the experimental design. *P*-values were regarded as significant at $\propto < 0.05$. The two focal species were analysed separately as differences in the responses were expected.

For aboveground biomass values, distance from talus, watering, and neighbour removal were regarded as fixed factors with block and all interactions of block with the fixed factors as random factors. Aboveground biomass data was natural log transformed for both species to meet assumptions of homogeneity of variance and normality. Initial plant size was analyzed using the above analysis plus current season grazing status to determine if experimental groups were equivalent at the beginning of the experiment and if herbivores preferred larger plants.

Analyses of leaf births and deaths were performed with the addition of current season grazing status as a fixed factor and initial plant size as a covariate. Only leaf demographic data from 2004 was analysed as no effects of the experimental treatments were recorded during the first growing season (2003). All interactions of block with the fixed factors were included, except the six-way interaction. Leaf births and deaths were natural log transformed (plus the addition of 1 as a constant to deal with zero values) to meet assumptions of homogeneity of variance and normality. Grazing was included as it was recorded *post hoc* to dramatically change the growth response of plants. This introduced unbalanced numbers into the experimental design as plants were not grazed and ungrazed in equal numbers. However, Proc MIXED provides correct standard errors and significance tests for fixed effects for unbalanced designs with random factors (Saavedra & Douglass, 2002).

The proportion of plants grazed in each block and the proportion of leaves grazed for individuals were analysed as split-split block ANOVAs, with distance from talus, watering, and neighbour removal as fixed factors. The same analysis was used for differences in soil nutrient availability, depth, and water content, and snowmelt date. All

data was natural log transformed to meet assumptions of homogeneity of variance and normality. We also performed a multiple logistic regression in SPSS to determine the important factors on grazing status for both species. Distance from talus, watering treatment, neighbour removal, and initial plant size were included in the model for grazing status.

RESULTS

Plant aboveground biomass

Overall effects of distance from talus, watering, and neighbour removal on plant aboveground biomass were small for both species. *Carex* individuals had greater aboveground biomass without neighbours for all combinations of distance to talus and watering (Fig 2-2 & Table 2-1). Neighbour removal also increased *Artemisia* aboveground biomass, especially for unwatered far from talus plants, but this effect was not statistically significant because increases were very small. Watered *Artemisia* plants were smaller near to talus and larger far from talus, and there was a synergistic interaction between these two factors (distance x water interaction; Fig 2-2 & Table 2-1). No other treatment effects or interactions were present for aboveground biomass for either species. There were no differences in initial size for either species for any treatment combination.

Neighbour removal had significant effects on soil nitrate availability, such that plots without neighbours had significantly higher nitrate compared to plots with neighbours (Fig. 2-3; ANOVA: $F_{1,84.8} = 5.05$, $P = 0.0272$). Soil nitrate availability was also greater

far from talus (ANOVA: $F_{1,94.1} = 9.05$, $P = 0.0034$). The increase in soil nitrate for plots without neighbours was much greater near to talus than far from talus, but the interaction between distance and neighbour removal was not significant (ANOVA: $F_{1,83.6} = 1.56$, $P = 0.2158$). There were no significant effects of any of the treatments on soil ammonium availability.

Differences in soil nitrate availability between distances may be related to soil depth and snowmelt dates for the two distances. Far from talus plots had significantly higher soil depth (near: 13.2 ± 1.6cm; far: 17.9 ± 1.6cm; ANOVA: $F_{1,42} = 10.16$, $P = 0.0027$) and earlier snowmelt (near: May 17th ± 2.2 days, far: May 11th ± 2.2 days; ANOVA: $F_{1,11} = 6.62$, $P = 0.0259$). Additionally, the watering treatment increased soil water content near to talus (unwatered: 61.3 ± 3.7%, watered: 70.3 ± 1.6%) but not far from talus (unwatered: 73.9 ± 3.0%, watered: 73.4 ± 2.5%; ANOVA: distance x water: $F_{1,34.3} = 4.60$; $P = 0.0391$).

Neighbour removal also increased tissue nitrogen content for plants (Fig. 2-4). For both species, C:N ratios were lower for plants grown without neighbours than for plants with neighbours present (ANOVA: *Artemisia*: $F_{1,91.6} = 15.17$, $P = 0.0002$; *Carex*: $F_{1,97} = 19.71$, $P < 0.0001$).

In addition to effects on target plants, neighbour removal also had effects on the behaviour of the herbivores in the system. Plants without neighbours were much more likely to be grazed (Fig. 2-5 & Table 2-2). The proportion of plants grazed decreased with distance from talus for *Artemisia,* while for *Carex* individuals that were watered were less likely to be grazed (Fig. 2-5 & Table 2-2). Watering also decreased the proportion of leaves grazed per plant for *Carex* while this effect was only slightly

significant for *Artemisia* plants. Herbivores also grazed preferentially on larger *Artemisia* plants (ungrazed: 4.9 initial leaves, grazed: 6.1 initial leaves; ANOVA: $F_{1,391} = 15.92$, $P = < 0.0001$), but not on larger *Carex* plants (ungrazed: 3.9 initial leaves, grazed: 3.7 initial leaves; ANOVA: $F_{1,344} = 1.75$, $P = 0.1873$). This difference between species may due to the size distributions of the two species: *Artemisia* plants ranged from 3 to 40 leaves, while *Carex* ranged from 2-8 leaves. Multiple logistic regressions (Table 3) were consistent with results above, and identified distance from talus, neighbour removal and initial plant size as important factors for grazing status of *Artemisia*, and watering and neighbour removal as important for *Carex*.

Plant size relationships

For *Artemisia*, the relationship between number of live leaves and plant size were positive for both leaf mass and rhizome mass at both distances from talus (Fig. 2-7). Regressions between leaf number and leaf mass were much stronger than those for rhizome mass, but a significantly positive relationship was still present.

Leaf births & deaths

Five-way interactions between distance from talus, watering, neighbour removal, grazing status, and initial plant size were present for *Artemisia* leaf births (ANCOVA: $F_{1,439} = 3.83$, $P = 0.0511$) and leaf deaths (ANCOVA: $F_{1,427} = 5.27$, $P = 0.0222$) (Appendix). While these cannot be fully interpreted in a biologically meaningful way, general trends can be summarized as follows. Near to talus plants that were ungrazed and unwatered had fewer leaf births with increasing initial size (Fig. 2-7). This relationship

was reversed when plants were watered or grazed, such that larger plants had more leaf births. Near to talus plants grown without neighbours had more leaf births than those with neighbours, and this difference generally increased with plant size. Far from talus the results become more complex, partly due to an absence of grazed *Artemisia* individuals at this distance. Plants without neighbours generally had more leaf births. For leaf deaths, grazed plants in general had more leaf deaths than ungrazed plants (Fig. 2-8).

For *Carex*, only the interaction between neighbour removal and plant size was significant (ANCOVA: $F_{1,367} = 6.16$, $P = 0.0135$) (Appendix). Large *Carex* plants with neighbours removed had fewer leaf births than smaller plants; this relationship was reversed when neighbours were present.

DISCUSSION

The response of both *Artemisia* and *Carex* plants to the experimental treatments depended on abiotic conditions and biotic variables as well as characteristics of the plants such as size (Fig. 2-9). We recorded opposing competitive and facilitative interactions neighbouring plants, as well as effects of historical and current season grazing and watering (Fig. 2-9).

Neighbour effects on soil nitrate

Neighbour removal resulted in competitive release for both species, measured as small increases of aboveground plant biomass in both species (Fig. 2-2). This may be

related to increased soil nitrate availability. There were significant increases in soil nitrate and plant leaf nitrogen content during this study when neighbours were removed (Figs. 2-3 & 2-4). While some of this nutrient increase can be accounted for by decaying roots or increased soil microbe mineralization and nitrogen-fixation that is associated with higher soil temperatures(Nilsson *et al*, 2002), it is likely that fewer plants are taking up nutrients. Alpine and arctic systems generally have little available soil nitrogen and nitrogen often limits primary productivity (Nilsson *et al*, 2002; Korner, 2003). Low soil temperatures mean limited chemical weathering and nitrogen fixation by soil bacteria (Nilsson *et al*, 2002; Bliss, 1971), and rapid uptake by plants and microbes result in little free nitrogen in the soil at any given time (van Wijk *et al*, 2003; Nordin *et al*, 2004). Many studies have shown that nitrogen addition can increase productivity (e.g. Cargill & Jefferies, 1984; Chapin *et al*, 1995) and influence community composition (Theodose *et al*, 1997; Chapin *et al*, 1995; Cornelissen *et al*, 2001; Nilsson *et al*, 2002) in alpine and arctic systems. This has also been demonstrated for our study system (Tait, 2002; D. Hik, unpublished data). The dominance of belowground interactions in alpine systems is also supported by the fact that plant biomass in these systems is predominantly belowground (Bliss, 1971; Fisk *et al*, 1998; Korner, 2003). In this system, approximately six times as much plant biomass (coarse roots) is present belowground to a depth of five centimeters as compared to aboveground (M. Mitchell, unpublished data). With fine roots included and roots from deeper soil, belowground biomass could easily be ten to twenty times greater. Also, competition for light is minimal in systems with low productivity and low stature vegetation (Wilson & Tilman, 1991; Goldberg & Novoplansky, 1997).

The presence of mosses and lichens could also have influenced the overall interaction effects that we observed. These two groups were retained in plots where neighbours were removed to reduce changes in soil temperature and maintain substrate structure. Mosses and lichens were likely to have competed for soil nutrients and water, while at the same time minimizing evaporation from the soil and fixing nitrogen from the atmosphere (Cornelissen *et al*, 2001). We were mainly interested in interactions between vascular plants, however there may be significant interactions between our focal species and the cryptogamic species in this system that could influence our results.

Neighbour effects on plant apparency & grazing

Neighbour removal also affected the probability of plants being grazed, which may have opposed the positive effects of increased soil nutrients. During the study, soil resources increased significantly with neighbour removal, especially near to talus (an approximate 2.5 times increase). However, aboveground biomass increases were small for both species. This may be partly due to the short duration of the experiment (2 growing seasons). It has also been suggested that plants in stressful habitats should not respond to short-term changes in resource levels (Grime, 1977; Graham & Turkington, 2000). However, we saw significant increases in leaf births for both species with changes in resources, and optimal growth rates of alpine plants are often quite similar to those of plants in more favourable environments (Korner, 2003). Alpine and arctic plants invest heavily in belowground structures, but we were not able to collect belowground biomass and cannot determine the degree to which increased underground allocation was

important for plants grown without neighbours. Regardless, plants without neighbours were more likely to be grazed.

There was an approximate doubling in the number of plants grazed when neighbours were removed for both species, and while we do not have direct measures, we assume grazing removed a significant proportion of the aboveground plant biomass. McIntire & Hik (2002) demonstrated 60% removal of foliage in this system for three common plant species, and additional herbivore exclosure studies resulted in significant increases in plant aboveground standing crop (McIntire & Hik, 2005; Korner, 2003). These plants have few leaves and little aboveground mass, therefore the complete loss (for *Artemisia*) or loss of a significant portion (for *Carex*) of two or three leaves represents a large portion of their photosynthetic capacity and can have significant effects on photosynthetic ability (Tait, 2002).

We inferred that plants without neighbours were more apparent to the mammalian herbivores present in the system, both from a lack of camouflage and an increase in size. It appears that visual cues are important for herbivores in this system since plants lacking camouflage and larger plants were grazed more, while larger leaves have also been shown to be preferred by pikas (S. Morrison, unpublished data). A number of studies have shown that the surrounding plant community can affect plant apparency and foraging behaviour in herbivores (Atsatt & O'Dowd, 1976; Brown & Ewel, 1987; Frid & Turkington, 2001; Milchunas & Noy-Meir, 2002) and that facilitation can occur through reduced consumer pressure (Bertness & Callaway, 1994; Callaway, 1995 & 2005). The effect of neighbours is not limited to vertebrate herbivores and has also been shown for invertebrates (Hjalten & Price, 1997; Hamback *et al*, 2000). Additionally, plants without

neighbours could be more palatable to herbivores due to higher tissue nitrogen content, and cafeteria-style feeding trials in this system have shown that pikas can distinguish between fertilized and unfertilized leaves (S. Morrison, unpublished data). Nevertheless, the fact that there were no differences in the proportion of leaves grazed per plant between neighbour removal treatments, suggests that differences in palatability were unlikely to account for differences in grazing.

The effect of neighbour removal on herbivore behaviour could influence the results of experiments attempting to quantify competition in natural systems. Neighbour removal designs have been extensively used for competition experiments involving plants in natural systems. If herbivores are not excluded from the system, and plants without neighbours are selectively grazed, then any conclusions about the intensity of competition for specific species will be suspect. Plant biomass losses to herbivores, or alternatively, compensation or overcompensation by grazed plants could seriously affect measures of competition. If species strongly selected for by herbivores are used in a study, strong competitive interactions may be present but may not be recorded as biomass measures due to losses from grazing. Meanwhile, individuals of unpalatable species can have greater release from competition, even if they are weaker competitors. Experiments where the focus is the cumulative effects of neighbours, where grazing is artificial or unselective, or where herbivores are excluded from the experiment, should be free of these problems.

Effects of grazing history & watering

Distance from talus and watering did not show strong effects on the aboveground biomass of either species (Fig. 2-2), even though there were large differences in soil nitrate availability, grazing pressure for *Artemisia*, soil depth, and growing season length. We expected that plants under high, long-term grazing pressure would be less able to respond to neighbour removal due to lower levels of stored resources. The lack of significant effects leads us to believe that there have been long-term adjustments by these individuals or that the clonal nature of the plants buffer them, at least in the short-term, to changing environmental conditions.

Watering did not show many significant effects on plant biomass (Fig. 2-2), which is evidence that water is not a limiting resource in this system, at least within the limits of this experiment. Depending on the snowmelt regime, soil moisture can be quite high throughout the growing season in alpine systems (Korner, 2003) and our level of increase may not have been large enough to cause changes in soil nutrients or plant water status. Water has been shown to control litter decomposition and soil microbe activity such as N mineralization and immobilization in arctic and alpine systems (Fisk *et al*, 1998; Bryant *et al*, 1998) but did not appear to have any effect on soil nutrients in our study. At dry microsites and at certain times of the year water may be limiting, but overall for this system it does not appear to be to be important.

Watering appeared to have non-intuitive effects on the grazing behaviour of herbivores in this system. Watered *Carex* plants were less likely to be grazed, and individuals of both species lost fewer leaves to herbivores when watered. This effect does not appear to be related to the nitrogen status of these plants as there were no

differences between watered and unwatered plants. These results may be due to other changes in plant chemistry including defensive compounds, as there is some evidence from agricultural species that watering can induce genes involved in plant defense (Subramanyam *et al*, 2006). However, most studies have seen increased defensive compound production in water *stressed* individuals (Estiarte *et al*, 1994; Pare & Tumlinson, 1999). Specific mechanisms for any possible changes in plant chemistry associated with watering are presently unknown.

Leaf births & deaths

While changes in plant aboveground biomass were modest over the course of the experiment, changes in leaf births and deaths were more responsive (Figs. 2-2, 2-8 & 2-9). Indeed, the maintenance of aboveground biomass despite loss of tissue to grazing appears to be due to plasticity in leaf initiation, especially in *Artemisia*. Since alpine plants are very rarely carbon-limited (Korner, 2003), light competition is minimal, and all aboveground plant material dies at the end of the growing season, it is probably not adaptive for these plants to greatly increase aboveground biomass when there are increases in soil resources.

That the response to grazing is greatest near to talus may suggest that these plants, consistently grazed from year to year, are better able to mobilize resources and respond to grazing events than those far from talus that are less frequently grazed. There are few studies of variation of plasticity within populations (Schlichting, 1986) but there is some evidence that this is possible: *Collimia* plants taken from disturbed sites exhibited more plasticity than those from adjacent meadows (Wilken, 1977) and genotypes of

Polygonum differ in their ability to respond along an environmental gradient (Zangerl & Bazzaz, 1983). Similarly, grazing has been shown to increase axillary shoot production or leaf turnover in two arctic salt-marsh graminoids *Puccinellia phryganodes* and *Carex subspathacea* (Bazely & Jefferies, 1989; Hik *et al*, 1991), and resource levels can also determine aboveground productivity (Cargill & Jefferies, 1984) and influence the response of plants to grazing (Hik *et al*, 1991).

There were significant differences between *Artemisia* and *Carex* individuals and their ability to respond to environmental change, which also demonstrates different strategies for tolerating grazing between plant growth forms. While *Artemisia* had highly plastic responses to the experimental treatments with plant size playing an important role, only one interaction of plant size with any of the experimental treatments was seen for *Carex*. *Artemisia* plants have multiple meristems with which to initiate new leaves that can become active after the loss of apical dominance following grazing (Huhta *et al*, 2000) while *Carex* leaves have basal meristems and can elongate older leaves, even if grazed.

While measures of biomass are the usual metric of plant performance in studies of plant interactions, and have been shown to be correlated with plant fitness (Aarssen & Clauss, 1992), our results show that leaf demography can also change significantly with experimental and environmental change. Therefore, using these measures can be of value in systems where plants are small and the growing season is short, although caution is needed when interpreting these changes. The long-term consequences of changes in leaf births, deaths, turnover and longevity for the fitness of plants has not been well defined. For example, grazing can significantly increase leaf births, yet compensation may not be

sufficient to balance tissue loss and photosynthetic capacity, resulting in a decline of fitness. The combination of both biomass and demography measures should give a better indication of a plant's response to perturbation as well as its resource status and fitness.

Conclusions

Our results suggest that there is a balance between resource competition and herbivory. The benefits of increased soil resources were opposed by the costs associated with the increased likelihood of being grazed (Fig. 2-9). These pressures may select for plants of intermediate size or those that preferentially allocate to underground organs, especially in areas with high grazing pressure, but the specific implications for population dynamics are still uncertain. Both species demonstrated adaptation to long-term grazing conditions and high levels of plasticity with respect to leaf demography in response to environmental change, but this plasticity was constrained by the morphological characteristics of the species and the harsh abiotic climatic conditions.

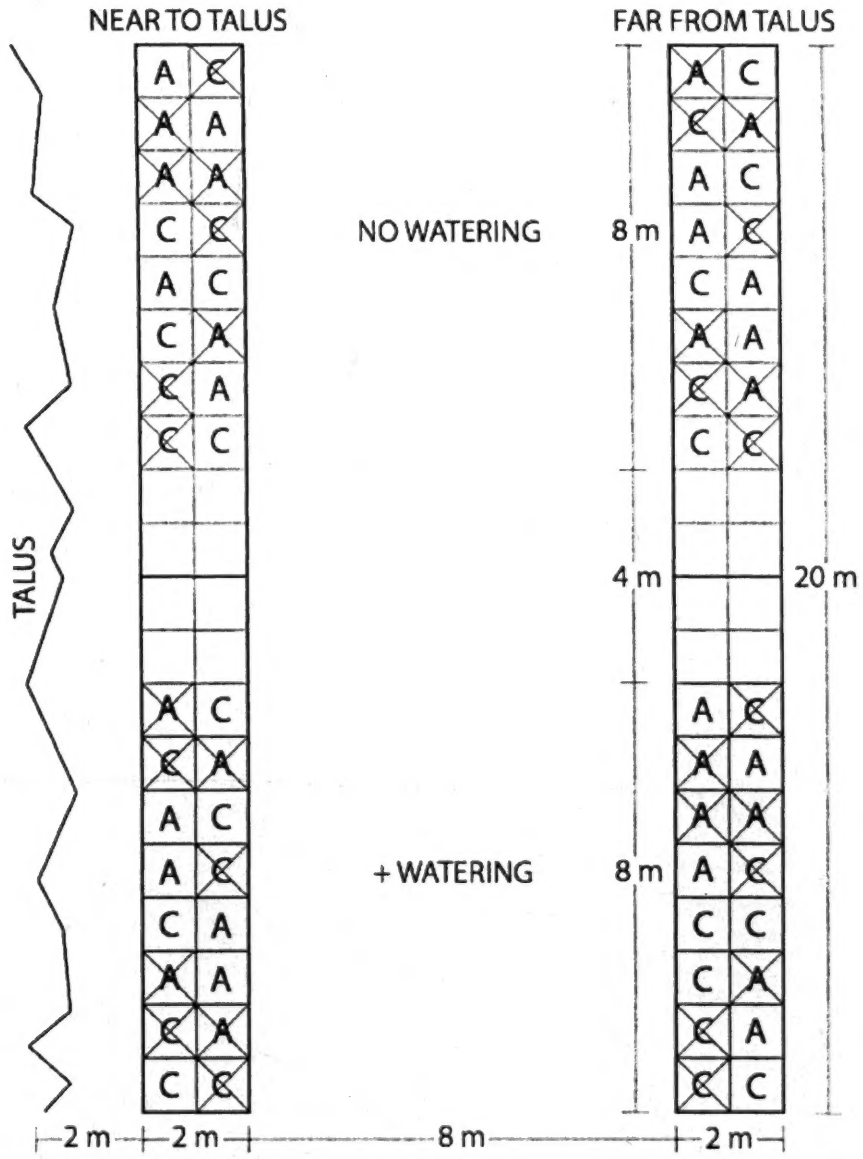


Fig. 2-1 – Schematic of a typical experimental block. Each individual square represents a 1m x 1m plot each containing one individual of one of the focal species. *Artemisia norvegica* individuals are represented by A's, *Carex consimilis* individuals by C's. Individuals that have had neighbours removed within a 25cm x 25cm square are indicated by crosses. The near to talus plots (within 2m of the talus margin) have had relative high historical grazing while those far from talus have had low historical grazing. Plants in the bottom half of each plot were watered (shaded squares) while those in the top half did not receive any supplemental precipitation.

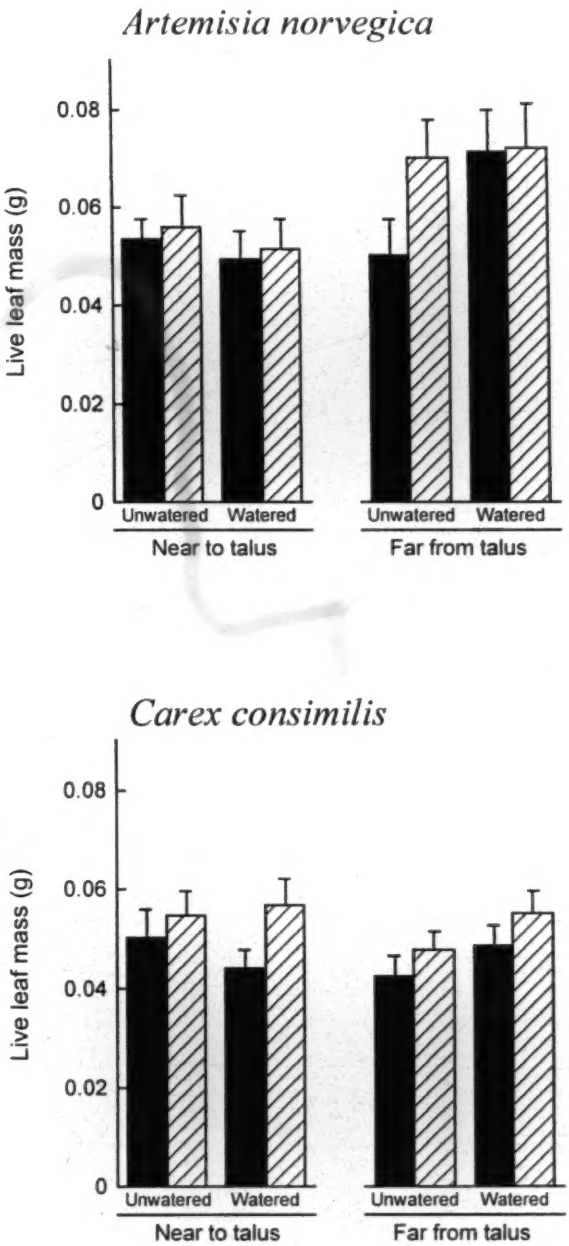


Fig. 2-2 – Live leaf mass for *Artemisia norvegica* and *Carex consimilis* individuals at the end of the second growing season (2004). Solid bars represent plants with neighbours present, hatched bars are plants with neighbours removed. Bars show mean values ± 1 SE.

Table 2-1 – General linear mixed models of the effects of distance from talus, watering, and neighbour removal on live leaf mass for *Artemisia norvegica* and *Carex consimilis* individuals at the end of the second growing season (2004). Bold values indicate significance at $P < 0.05$; degrees of freedom were calculated using Satterthwaite's method.

	Artemisia norvegica		*Carex consimilis*	
Level	$F_{(numdf,dendf)}$	*P*-value	$F_{(numdf,dendf)}$	*P*-value
Distance	$3.15_{(1,441)}$	0.0767	$0.87_{(1,387)}$	0.3526
Watering	$0.21_{(1,441)}$	0.6440	$0.49_{(1,387)}$	0.4822
Dist x Water	**$5.81_{(1,441)}$**	**0.0163**	$1.97_{(1,385)}$	0.1608
Neighbours	$0.86_{(1,28)}$	0.3612	**$5.39_{(1,389)}$**	**0.0208**
Dist x Neighbours	$1.78_{(1,441)}$	0.1830	$0.21_{(1,387)}$	0.6487
Water X Neighbours	$0.63_{(1,441)}$	0.4294	$0.62_{(1,386)}$	0.4302
Dist x Water x Neigh	$2.93_{(1,447)}$	0.0877	$0.24_{(1,387)}$	0.6249

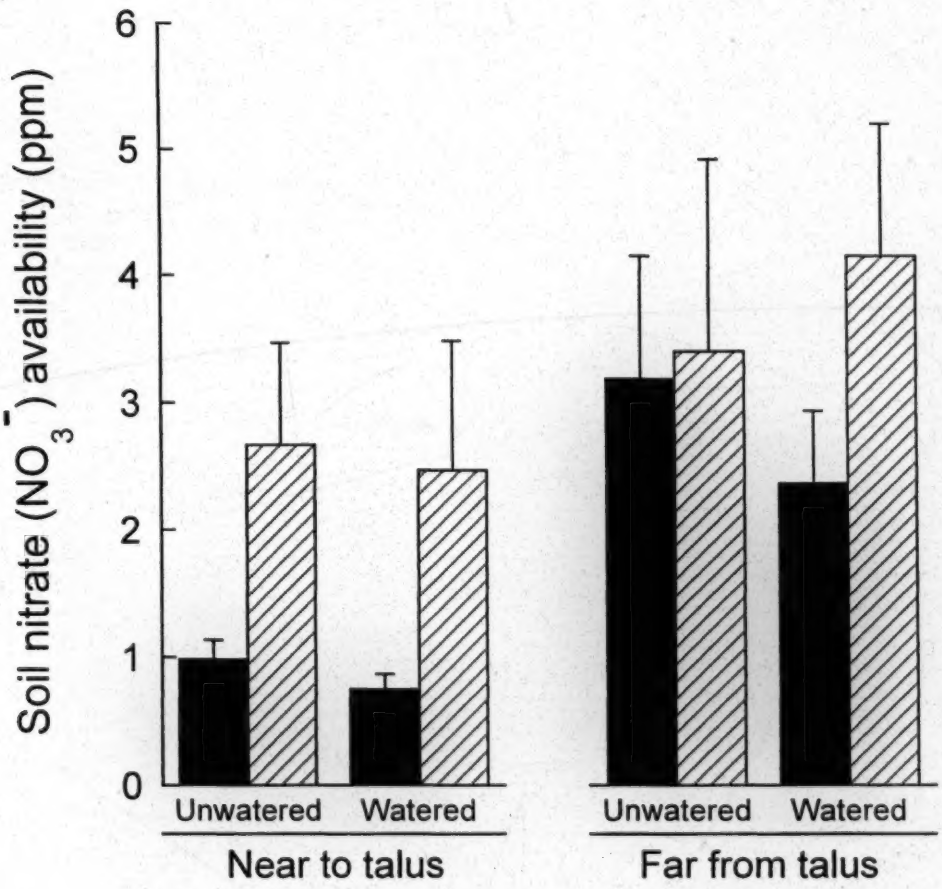


Fig. 2-3 – Plot soil nitrate ion (NO_3^-) availability during the 2004 growing season. Solid bars represent plots where neighbours were present, hatched bars plots where neighbours were removed. Values were determined from liquid extracts of ion exchange resin that was placed in nylon bags and buried in plots for two months of the second growing season of the study. As such they are not true values of soil nitrate concentrations but represent qualitative differences between the different treatment combinations. Bars show mean values ± 1 SE.

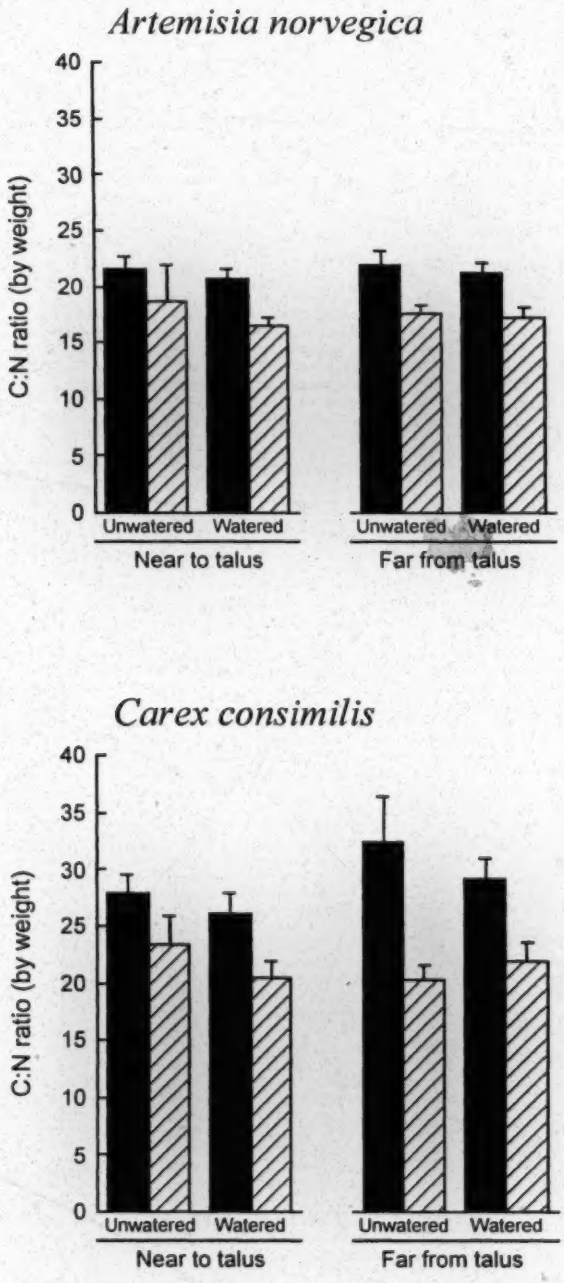


Fig. 2-4 – Leaf tissue carbon:nitrogen ratios by weight for *Artemisia norvegica* and *Carex consimilis* individuals at the end of the second growing season of the study (2004). Solid bars represent plants with neighbours present, hatched bars plants with neighbours removed. Bars show mean values ± 1 SE.

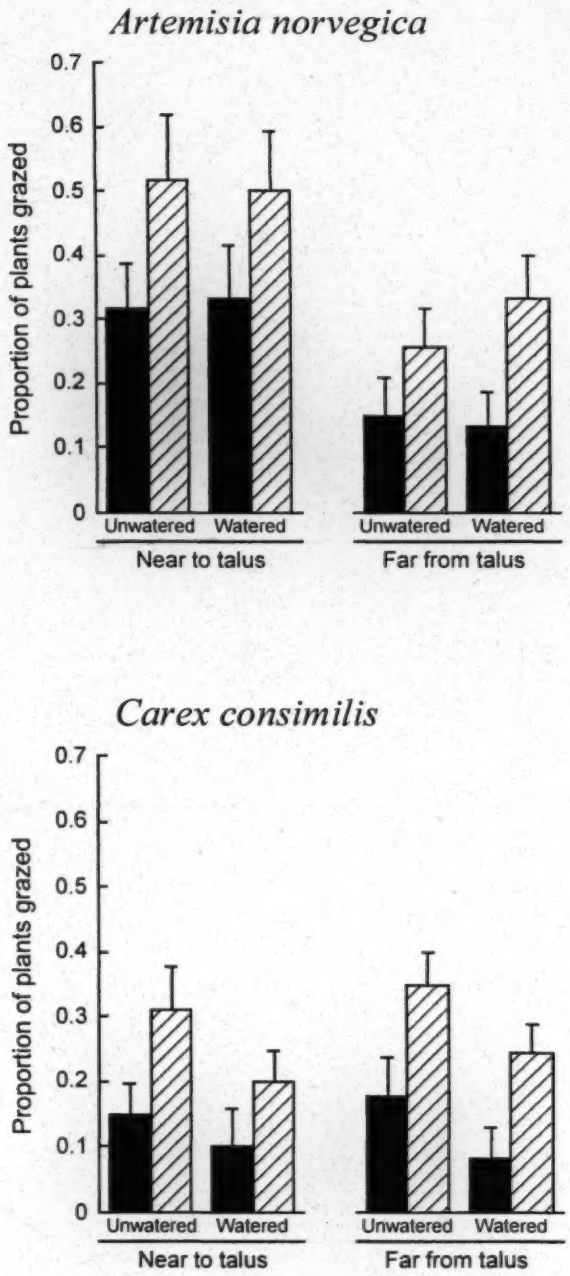


Fig. 2-5 – Proportion of *Artemisia norvegica* and *Carex consimilis* plants grazed (per block) during the 2004 growing season. Solid bars represent plants with neighbours present while hatched bars represent plants without neighbours. Bars show mean values ± 1 SE.

Table 2-2 – General linear mixed models of the effects of distance from talus, watering, and neighbour removal on the proportion of individuals grazed (per block) and the proportion of leaves grazed (per individual) for *Artemisia norvegica* and *Carex consimilis* individuals during the 2004 growing season. Bold values indicate significance at $P < 0.05$; degrees of freedom were calculated using Satterthwaite's method.

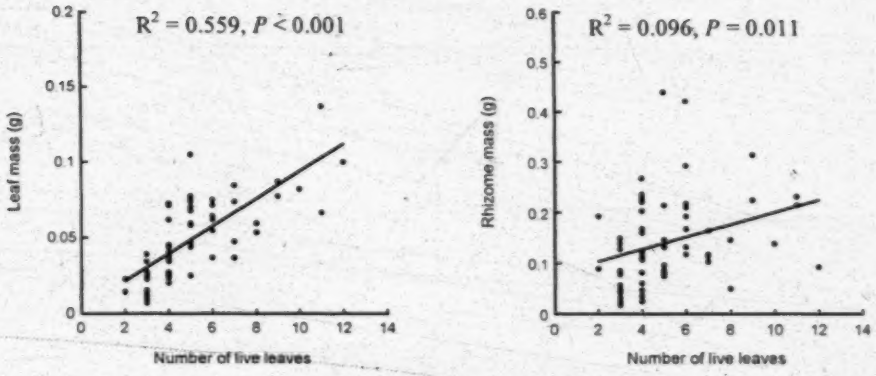
	Artemisia norvegica				*Carex consimilis*			
	Proportion Ind. Grazed		Proportion Lvs. Grazed		Proportion Ind. Grazed		Proportion Lvs. Grazed	
Level	$F_{(numdf,dendf)}$	*P*-value	$F_{(numdf,dendf)}$	*P*-value	$F_{(numdf,dendf)}$	*P*-value	$F_{(numdf,dendf)}$	*P*-value
Distance	**$7.06_{(1,14)}$**	**0.0188**	$0.93_{(1,143)}$	0.3376	$0.60_{(1,112)}$	0.4394	$0.06_{(1,72.6)}$	0.8074
Watering	$0.27_{(1,84)}$	0.6080	$3.24_{(1,134)}$	0.0741	**$6.18_{(1,112)}$**	**0.0144**	**$4.19_{(1,72.1)}$**	**0.0443**
Dist x Water	$0.01_{(1,84)}$	0.9214	$0.48_{(1,144)}$	0.4913	$0.02_{(1,112)}$	0.8935	$2.67_{(1,75)}$	0.1064
Neighbours	**$12.14_{(1,84)}$**	**0.0008**	$0.07_{(1,136)}$	0.7937	**$21.35_{(1,112)}$**	**<0.0001**	$0.66_{(1,71.4)}$	0.4199
Dist x Neigh	$0.87_{(1,84)}$	0.3531	$0.11_{(1,138)}$	0.7355	$0.49_{(1,112)}$	0.4850	$2.28_{(1,72.6)}$	0.1353
Water x Neigh	$0.35_{(1,84)}$	0.5583	$0.30_{(1,143)}$	0.5837	$0.05_{(1,112)}$	0.8273	$0.00_{(1,69.3)}$	0.9478
D x W x N	$0.38_{(1,84)}$	0.5406	$0.03_{(1,139)}$	0.8592	$0.01_{(1,112)}$	0.9124	$0.10_{(1,70.5)}$	0.7522

Table 2-3 – Multiple logistic regression of the grazing status of *Artemisia norvegica* and *Carex consimilis* plants (during 2004) on distance from talus, watering, neighbour removal, and initial size. (Nagelkerke R^2 for *Artemisia*: 0.147, for *Carex*: 0.085, both were significant to $P \leq 0.001$ by a χ^2 test).

	Artemisia norvegica	*Carex consimilis*
Variable	Odds ratios†	Odds ratios†
Distance from talus	0.352***	1.122 NS
Watering	1.075 NS	0.527*
Neighbour removal	2.356***	2.624***
Initial size of plant	1.139**	0.825 NS

† Wald test statistic; ***$P \leq 0.001$; **$P \leq 0.01$; *$P \leq 0.05$; NS = not significant.

Near To Talus



Far From Talus

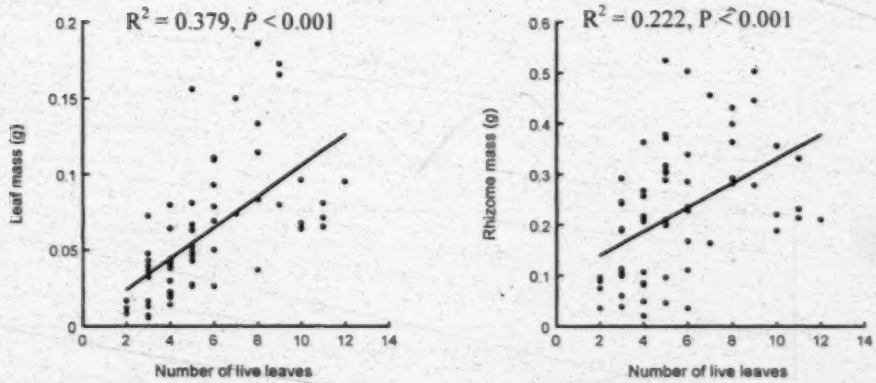


Fig. 2-6 – Relationships of number of live leaves with leaf mass and rhizome mass for *Artemisia norvegica* individuals both near to talus and far from talus. Note the different scales.

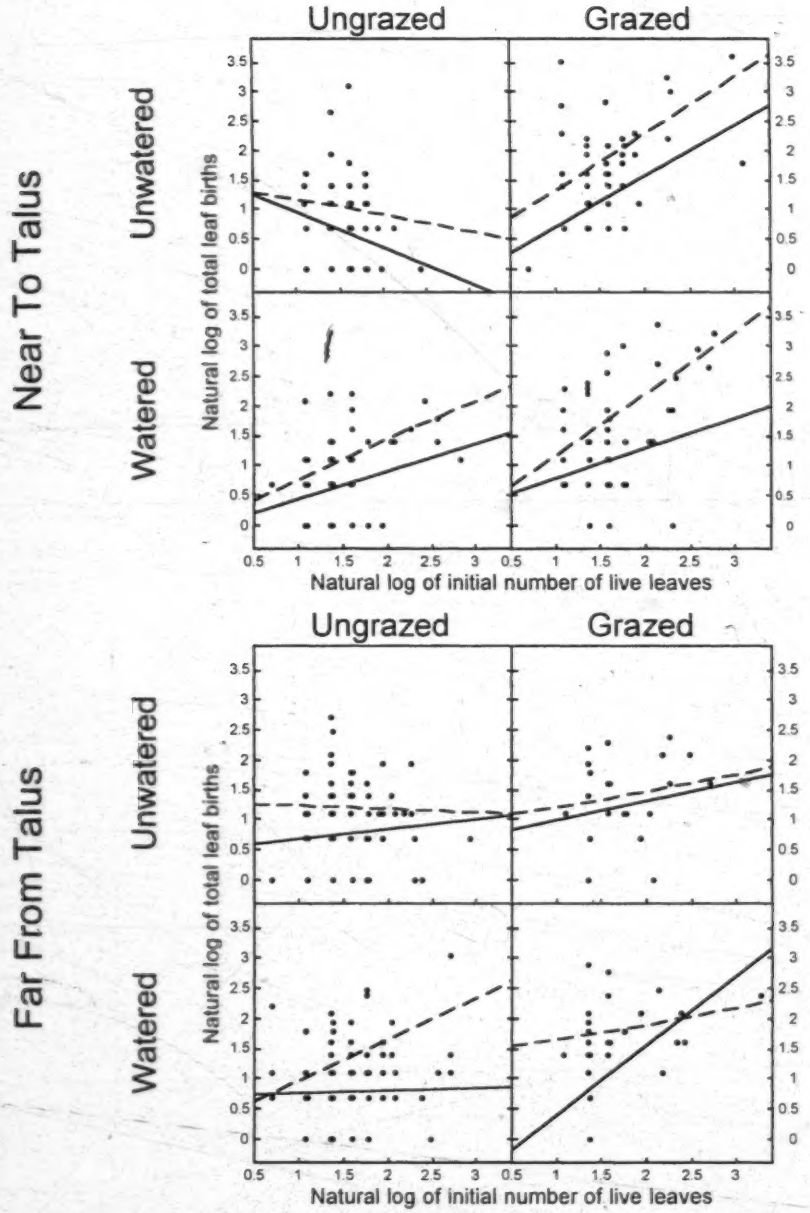


Fig. 2-7 – Relationships between initial plant size (# of live leaves) and total number of leaf births over the 2004 growing season for *Artemisia norvegica* individuals. Solid lines are least square mean regression lines for plants with neighbours (solid data points), dashed lines those for plants without neighbours (outlined data points). Values are in natural logs of raw data. The x-axis scale for plants without neighbours was adjusted slightly smaller than that of plants with neighbours so that data points could be compared between the two treatments.

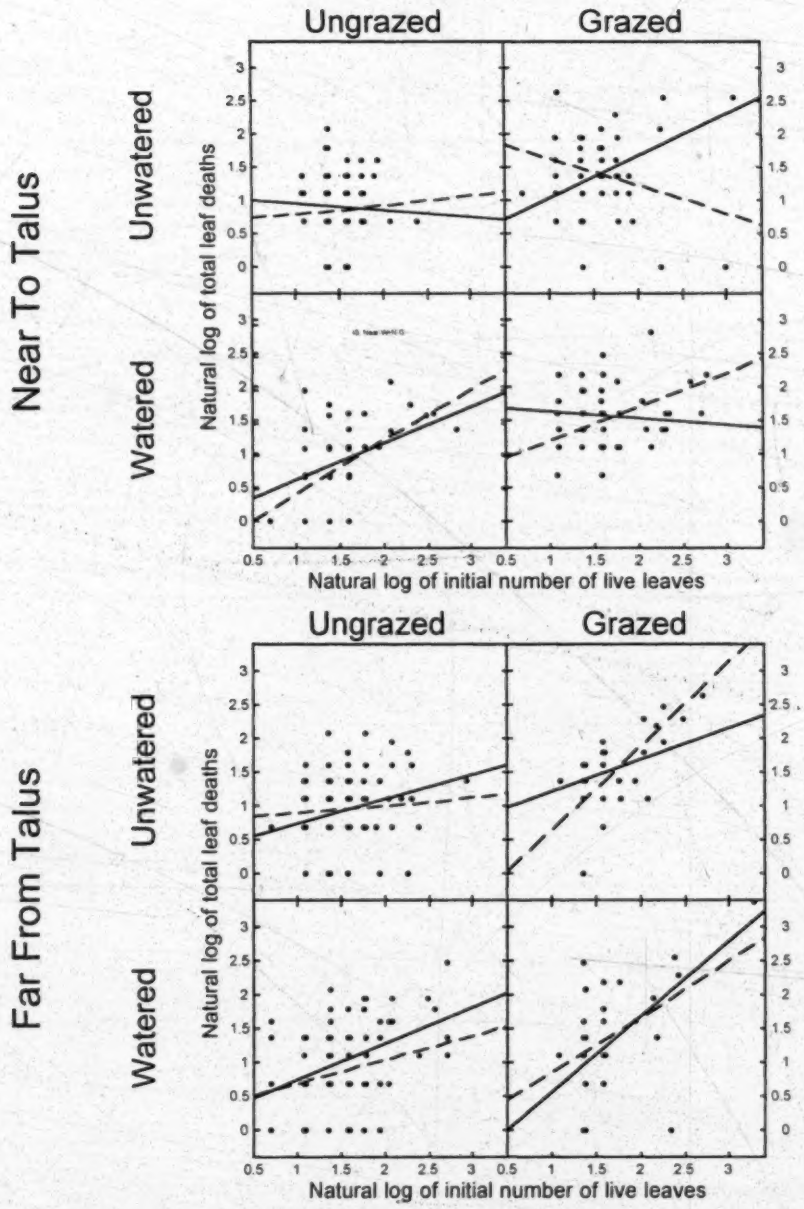


Fig. 2-8 – Relationships between initial plant size (# of live leaves) and total number of leaf deaths over the 2004 growing season for *Artemisia norvegica* individuals. Solid lines are least square mean regression lines for plants with neighbours (solid data points), dashed lines those for plants without neighbours (outlined data points). Values are in natural logs of raw data. The x-axis scale for plants without neighbours was adjusted slightly smaller than that of plants with neighbours so that data points could be compared between the two treatments.

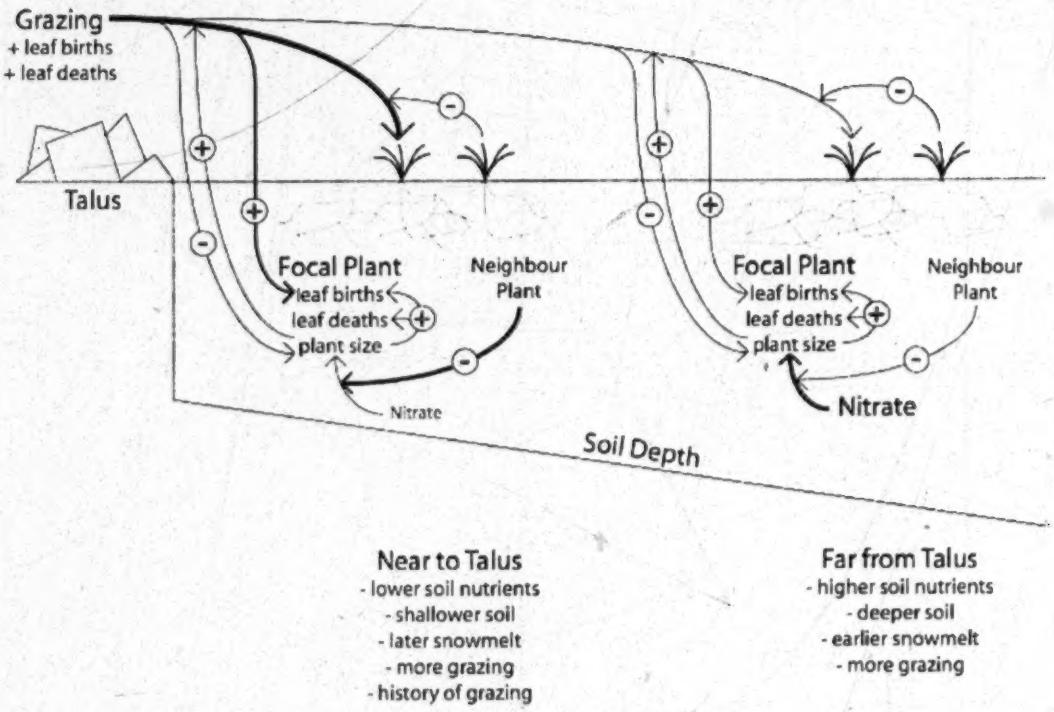


Fig. 2-9 – Conceptual diagram of the relationships between the abiotic and biotic variables with various plant characteristics during the study. The strength of the relationships is indicated by the thickness of the arrow. Neighbouring plants had negative effects on both nutrient availability for focal plants and the chance of being grazed. Plant size increased the chance of being grazed, while grazing decreased plant size. Grazing increased leaf births and deaths, but the direct effects of grazing on leaf deaths were not included in the diagram.

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CHAPTER 3

LOCAL SCALE ENVIRONMENTAL CONTROLS ON COMPETITION, FACILITATION AND SPCEIS ABUNDANCE IN A SUBARCTIC-ALPINE PLANT COMMUNITY

INTRODUCTION

The nature of interactions among plants can vary from competitive to facilitative dependent on the local biotic and abiotic conditions (Callaway & Walker, 1997; Pugnaire & Luque, 2001). Numerous studies have demonstrated the presence and importance of competition in a range of systems (Goldberg & Barton, 1992), with subsequent focus on competition strength along environmental gradients (Van der Wal, 2000; Keddy, 2001) and the effects of competition on community structure (Hairston *et al*, 1960; Goldberg & Barton, 1992; Kokkoris *et al*, 1999). Facilitation has not had as much attention in ecology as it can be masked by strong competitive interactions (Brooker & Callaghan, 1998; Pugnaire & Luque, 2001), but recent work has highlighted the presence and importance of facilitative interactions under a variety of conditions (Bertness & Callaway, 1994; Callaway *et al*, 1996; Pugnaire *et al*, 1996; Brooker & Callaghan, 1998; Pugnaire & Luque, 2001; Bruno *et al*, 2003; Rand, 2004; Callaway *et al*, 2005).

A number of environmental variables and plant characteristics have been shown to affect the strength of competition, including plant age (Callaway & Walker, 1997), plant size (Weiner, 1993; Horvitz & Schemske, 2002), species identity (Aksenova *et al*, 1998; Cahill, 2002; Klanderud & Totland, 2005), herbivory (Bonser & Reader, 1995;

Gurevitch *et al*, 2000; Hamback & Beckerman, 2003), productivity and aboveground biomass (Goldberg *et al*, 1999; Sammul *et al*, 2000), disturbance (Ellison, 1987; Campbell & Grime, 1992), nutrient availability (Campbell & Grime, 1992; Pugnaire & Luque, 2001), and soil depth (Vanauken *et al*, 1994). Yet in some cases relationships between these gradients and the strength of plant interactions are weak or nonexistent (DiTommaso & Aarssen, 1991; Reader *et al*, 1994; Belcher *et al*, 1995; Peltzer *et al*, 1998).

While a large amount of work has focused on the various abiotic and biotic factors influencing competition, the processes controlling the presence and strength of facilitative mechanisms are less well understood. Numerous studies have demonstrated that the presence and importance of facilitation compared to competition increases as "abiotic stress" increases, often along a transect of elevation (Oksanen, 1992; Brooker & Callaghan, 1998; Callaway *et al*, 2002; Choler *et al*, 2001; Pugnaire & Luque, 2001 but see Goldberg *et al*, 1999; Cavieres *et al*, 2005). And while "stress" can include various environmental variables (i.e. *elevation*: Choler *et al*, 2001; Callaway *et al*, 2002; *nutrient availability*: Grime, 1977; Campbell & Grime, 1992; Pugnaire & Luque, 2001; *soil depth*: Belcher *et al*, 1995; *soil moisture*: Callaway *et al*, 1996; Brooker & Callaghan, 1998) there has been little work to look at the relationships between specific environmental variables and the balance between competition and facilitation.

In arctic and alpine systems the major limitation to plant growth is the abiotic environment (Chapin, 1987), which is characterized by extreme climatic conditions (Brooker & Callaghan, 1998; Olofsson *et al*, 1999; Korner, 2003). Therefore, the main proposed mechanism for facilitation in these systems is shelter from the harsh climate by

neighbouring plants (Bertness & Callaway, 1994; Kikvidze & Nakhutsrichvili, 1998), although reduction of consumer pressure by neighbours can also be important (Callaway *et al*, 2005). Competition can also be present in these systems and is associated with decreased soil nutrients (Olofsson *et al*, 1999; Klanderud & Totland, 2005), decreased soil and meristem temperatures from shading (Fetcher, 1985; Havstrom *et al*, 1993), and the spatial dominance of dense roots (Korner, 2003). While the local and microhabitat variables that are important in determining species abundances have been investigated in many systems for numerous species, they are rarely related to the balance between competition and facilitation and the strengths of these interactions. Specifically, these relationships are unknown in arctic and alpine systems.

The aim of this study was to determine what local scale environmental factors control competition/facilitation intensity for two common species present in a subarctic-alpine meadow. We then wanted to determine the relative importance of these interactions on species abundance. We chose a number of variables that have previously been shown to influence the direction and strength of plant interactions, as well as variables that have been shown to influence plant performance and species distribution in arctic and alpine systems (Chapin, 1987; Korner, 2003). This included aboveground standing crop, vegetation cover, herbivory, soil depth, soil nutrient availability, and timing of snowmelt (Molau, 1993). The influence of neighbours on plant growth was ascertained using a neighbour removal approach over two growing seasons and then related to the environmental factors using regression trees.

METHODS

Study area and species

This study was conducted in subarctic-alpine meadows of the Ruby Range mountains (61°13'N, 138°16'W, elevation 1750m) of the southwest Yukon Territory, Canada. The snow-free growing season generally runs from mid-June to late August. For 1995-2000 mean winter temperatures were -12°C (Oct. – April), and mean summer temperatures were 11°C (June – Aug.), with a mean annual precipitation of 250mm.

The study area consists of a matrix of meadows that surround isolated rock boulder fields. These patches are formed by frost weathering of the bedrock and are generally known as block fields or felsenmeers (Washburn, 1979) but will be referred to as talus patches in this paper. The plant community is dominated by hybrid willow shrubs (*Salix* spp.), sedges (predominantly *Carex consimilis* Holm), *Dryas octopetala* L., *Cassiope tetragona* (L.) D. Don, (Cody, 2000) and various perennial herbs.

The main herbivores present are small mammals, including hoary marmots (*Marmota caligata*: Rodentia), collared pikas (*Ochotona collaris*: Lagomorpha), and arctic ground squirrels (*Spermophilus parryii*: Rodentia). Insect presence and herbivory aboveground is minimal and plant damage from insects is rarely observed (Hik *et al*, 2003; Mitchell, pers. obs.), however belowground herbivory has not been quantified in this system. Pikas (Lagomorpha) are small, rock-dwelling, generalist, central-place foraging herbivores of alpine areas. As central-place foragers they nest within the boulderfields and graze mainly within 6m of the margin of the talus, with plants inside

2m of the talus margins consistently grazed from year to year (Huntly, 1987; McIntire & Hik 2002 & 2005).

Two common forage plants used by pikas were chosen for this study. *Artemisia norvegica* Fries. (Asteraceae) is a small perennial, rhizomatous herb with a cespitose growth form and apical meristems. *Carex consimilis* Holm. (Cyperaceae) is the dominant sedge species of the community, and typical of graminoids has basal meristems. For this paper we will refer to each species by it genus name. Both species are used extensively by mammalian herbivores, exhibit clonal growth and were present in sufficient numbers throughout the study area and along the grazing gradient to allow individuals to be identified within reasonably sized plots. These two species should also respond to abiotic and biotic changes within two seasons, and more quickly than woody species.

Experimental Design

A split-split block design was used to investigate the effects of distance from talus and watering on plant interactions (see Chapter 2). Fifteen blocks were located on an east facing slope with several large talus patches. Each block was located parallel to the talus patch edge and contained two plots near to the talus (within 2m of the margin) and two plots far from the talus margin (8m from the near to talus plots) (Fig. 3-1). These two distances incorporated two levels of the long-term grazing gradient present in this system; near to talus plots have experienced historically high grazing levels while those far from talus have experienced lower grazing pressure (McIntire & Hik, 2002 & 2005). This distance treatment also incorporated other differences including soil depth, soil nutrient availability, and community composition (see Results). Half of the plots at both

distances within a block were watered over the course of the study but this did not have any measurable effect on the direction or outcome of the plant-plant interactions in the plot (see Chapter 2), so all plants were pooled into the two distance classes regardless of water treatment.

Plant Interactions

A neighbour removal approach was used to observe the outcome and strength of plant-plant interactions in this system. Each plot was divided into twenty 1m x 1m quadrats and the closest individual to the center of each quadrat of one of the focal species was identified (Fig. 3-1). The four squares between the paired plots at the same distance from talus were not used unless individuals could not be found in the first sixteen squares. This resulted in eight individuals of either species in each plot. For half of these plants all aboveground neighbour biomass within a 0.25m x 0.25m square around the focal individual was removed. Belowground roots were severed with a sharp knife along the same boundary around the focal individuals. The other half of the plants retained their neighbours but roots were severed to control for nutrient input from decaying roots. Above-ground neighbour regrowth was reclipped and roots severed three times during the growing seasons of both 2003 and 2004.

At the end of the second growing season all aboveground biomass of the focal plants was collected, dried to constant weight at 70°C and weighed to 0.0001g. Due to the nature of the alpine soils, the dense roots, and the clonal growth form of the species, it was not feasible to collect belowground roots.

To quantify the outcome and strength of the plant-plant interactions competitive response was calculated as the negative value of the log-response ratio (Cahill, 1999), which is related to relative competition intensity (Weigelt & Jolliffe, 2003). It is calculated as:

$$- \text{Natural log} \left(\frac{NP}{NR} \right)$$

where NP is the mean plant response with neighbours present and NR is the mean plant response with neighbours removed. Log response ratio is a relative measure of competition response that is symmetrical around zero and is therefore appropriate when investigating the balance between competition and facilitation. Relative measures remove possible confounding of direct effects of the environment on the response variable (Grace, 1995; Goldberg *et al*, 1999). The negative sign was added so that facilitative interactions provide positive values, and competition negative values. The metric was calculated based on aboveground biomass for each target plant. Within each plot the average value of the four individuals without neighbours (NR) was compared to the average of the four individuals whose neighbours were present (NP). This gave a single value for the plant interaction outcome for each species within each plot.

Plot Variables

Abiotic variables measured for each plot included soil depth, snowmelt date, and soil nitrogen (nitrate and ammonium) availability (Table 3-1). Soil depth was measured at four places (1, 3, 5, and 7m from the outside end) in each plot by sliding a thin metal

probe into the soil in three places 5 cm apart. The average of these 3 values was calculated for each location, and the average of all 4 location was calculated for each plot. Snowmelt date was determined by placing small iButton (Maxim Integrated Products, Sunnyvale, CA) dataloggers (n = 48) in plots just below the moss layer at the end of the growing season of 2003. Dataloggers were recovered at the beginning of the growing season in 2004 and snowmelt date determined where large diurnal fluctuations in temperature appeared. No effect of neighbour removal was observed on snowmelt date (Chapter 2). Soil nutrient availability was determined by using ion exchange resin bags, a method that simulates nutrient uptake by plant roots (Qian & Schoenau, 2002). Eight grams of DOWEX MR-3 mixed bed ion exchange resin (Aldrich Chemical Company; Milwaukee, WI.) were placed in nylon bags and prepared according to the methodology described by Thiffault *et al* (2000). Single bags were placed in plots of each treatment combination in each block (240 bags total - 30 in each treatment combination) 10cm beneath the soil surface for 6 weeks during the 2004 growing season. A large number of the bags were lost to marmot activity over the summer (84 near to talus; 53 far from talus). Remaining bags were removed on August 8th and were air dried before extraction. Ions captured by the resin were extracted by agitating the resin in 100ml of a 2N NaCl solution for 90 minutes, and the subsequent solution analysed for nitrate and ammonium ion concentration with a Dionex 600 Ion Chromatograph (Dionex Corporation; Sunnyvale, CA) and a Technicon Autoanalyzer II (Technicon Industrial Systems; Tarrytown, NY), respectively. Nutrient results are therefore presented as concentrations (ppm) of nitrate and ammonium present from this liquid extract. Only values from bags placed in plots with neighbours present were used in the analysis.

Biotic variables collected for each plot included composition and aboveground standing crop of vascular plants. For each plot at the same four locations where soil depth was measured, vascular and non-vascular plant species cover within a 0.3m x 0.3m quadrat was recorded. Vascular plants were identified to species, while non-vascular plants were recorded as either mosses or lichens. From the community composition data, indices of species richness were calculated following McCune & Grace (2002). Aboveground standing crop was determined by collecting all of the clippings from the initial neighbour removals. Live plant biomass was sorted from litter, dried at 70°C for three days to constant weight, and weighed to 0.0001g. Belowground plant biomass measures were not taken for any of the plots.

Data Analysis

Differences in abiotic variables between the two distances from talus were determined using general linear mixed models in SPSS 11.0.4 for Macintosh (SPSS Inc., 2005) with distance as a fixed factor and block as a random factor. To determine if species composition was different between the two distances, blocked multi-response permutation procedures were performed (MRBP) in PC-Ord 4.30 using Euclidean distances (MjM Software, Gleneden Beach, OR).

Plots at the two distances from talus were significantly different in composition as well as abiotic variables such as soil depth, soil nitrate availability, grazing history, and timing of snowmelt (see Results). Therefore to reduce the chance that interaction strength would be associated with abiotic variables when actually due to compositional

differences, plots from the two distances to talus were analysed separately. The results for *Carex* and *Artemisia* were also considered separately.

Regression Tree Analysis

Relationships between the variables were examined using regression trees, part of a pair of techniques usually referred to as CART (classification and regression trees). CARTs are non-parametric binary recursive partitioning procedures that progressively split data in a binary way into progressively more homogenous groups based on the one predictor variable that explains the greatest deviance in the data set at each step (Crawley, 2002). Variables can be chosen for splits multiple times within a single analysis, which makes CART very powerful at detecting complex and non-additive effects that linear additive models are poor at detecting (Karels *et al*, 2004). No assumptions about data distribution are required, and the method is not influenced by missing data, outliers, or monotonic transformations of the descriptor variables (Breiman *et al*, 1984, De'ath and Fabricius, 2000). CARTs offer an intuitive and clear picture of the structure of data and interactions among variables. They are ideal for complex ecological data (De'ath & Fabricius, 2000) and have been shown to be equal to or more effective than other methods such as multiple regression (Wietlisbach, 1999; De'ath & Fabricius, 2000), logistic regression (Vayssieres *et al*, 2000), and discriminant function analysis (Karels *et al*, 2004). Regression trees are also much better at detecting complicated interactions, non-additive effects of predictor variables and are able to minimize the effect of collinear variables better than parametric linear models (Karels *et al*, 2004). While extensively used in medicine for clinical risk assessments, they have only recently been recognized

by ecologists for use in such roles as community distributions (De'ath & Fabricius, 2000) and the effect of land-use changes on species abundance (Mankin, 1999).

Average values for competitive response, soil depth, soil nitrate and ammonium availability, aboveground standing crop, vegetation cover, proportion of *Carex* and *Artemisia* individuals grazed, and snowmelt were calculated for each plot. Due to a limited number of dataloggers and loss of resin bags to marmot disturbance, some plots were missing values. Therefore the average value for similar treatments was used to fill in these missing values, which permitted these plots to be included in regression tree analysis. The two plots either near to talus or far from talus within a block (Fig. 3-1) were not independent of each other, but were probably positively correlated (i.e. they were more similar to each other than other plots at that distance in other blocks). As a consequence, the slope of any relationship between abiotic and biotic variables and competition strength will be underestimated using regression analysis (*i.e.* it will be more difficult to detect a significant relationship between the two variables (Underwood, 1997)). The consequence of this non-independence should be that only the strongest relationships will be detected. It should also be noted that plots within separate blocks were often as close to (i.e. 4m apart) plots in different blocks as they were to their paired plot. The statistical method utilized in this study (classification and regression trees - CART) should also minimize the consequences of this problem, such that only the most important relationships will be emphasized.

Seven variables for each plot were used to predict the outcome of plant-plant interactions in each plot. Pearson correlations were used to examine all seven variables for independence, however no two variables were strongly correlated (i.e. Pearson

correlation > 0.5) in the data set for either distance, therefore all were retained for subsequent analysis.

Regression trees were constructed between the environmental variables and plant interaction values using the R statistical program (The R Foundation for Statistical Computing, 2005) with cross validation performed in CART 5.0 (Salford Systems, San Diego, CA). For both species at both distances, plots were split based on competitive response as explained by the seven environmental and biotic variables. Additional trees were formed by splitting plots based on the abundance of *Artemisia* and *Carex* with the seven environmental variables and values of competitive response for the two species. In this case vegetation cover values included all species other than *Artemisia* or *Carex*. In the analysis, plots were split until an additional split would have resulted in less than 5 plots in a terminal group. To determine if terminal splits were necessary, plots of deviance explained for each specific split were examined and validation procedures were performed as suggested by Breiman *et al* (1984).

RESULTS

Differences between distances from talus

The two distances differed in soil depth, snowmelt date, nitrate availability, and the proportion of *Artemisia* individuals grazed (Table 3-1). Community composition (MRBP, $P = 0.0015$; $a = 0.0751$) was also different between distances. Diversity indices for vascular plants at both distances are presented in Table 3-1.

Regression trees – competitive response

Artemisia: Near to talus, plants present in plots with low nitrate availability (< 0.75 ppm) experienced facilitation (0.686) and those with higher nitrate availability showed weak competition, the opposite of what was expected (Fig. 3-2a). Within plots with higher nitrate availability, those with less than 31.5% plant cover had weak facilitation (0.193), while with greater cover competition was present (-0.227). Far from talus, soil depth explained the most deviance, plots with soil depth between 14.3 cm and 18.5 cm had the strongest competition (-0.812), while on either side of this either weak competition or facilitation was present (Fig. 3-2b). Within plots with deep soil, nitrate availability was important; those with lower nitrate availability than 2.81 ppm showed facilitation while those with higher availability had weak competition.

Carex: Near to talus plots with lower ammonium availability (< 2.07 ppm) had weak facilitation while those with higher availability had competition (-0.432) (Fig. 3-2c). Within plots with higher ammonium availability, those with standing crop less than 37.9 g/m^2 had strong competition (-0.828). Plots with higher standing crop had strong competition when the snowmelt date was before May 17, otherwise competition was weak (-0.163). Far from talus grazing within plots results in lower intensities of competition (-0.089 vs. -0.427) (Fig. 3-2d). For plots where plants were grazed, those with low ammonium (< 3.09ppm) and low standing crop (< 56 g/m^2) had competition (-0.578), otherwise weak facilitation was present. The relationship between ammonium was opposite between the two distances from talus: facilitation near to talus and competition far from talus with low ammonium availability.

Regression Trees – Species Abundance

Artemisia: Near to talus *Artemisia* abundance was best predicted by plant cover, the competitive response of *Artemisia*, and soil depth (Fig. 3-3a). *Artemisia* cover was greatest when the cover of other species was greater than 46%. When cover was lower, the highest *Artemisia* abundances occurred when soil depth was greater than 10.8 cm and competition was present (competitive response < -0.049).

Far from talus the greatest abundance of *Artemisia* occurred when standing crop was greater than 100.3 g/m^2 (Fig. 3-3b). Within plots with lower values of aboveground standing crop, those with a snowmelt before May 14 and soil deeper than 19.7 cm had the highest *Artemisia* cover.

Carex: Similar to *Artemisia*, vegetation cover was important in predicting *Carex* cover near to talus (Fig. 3-3c). Plots with greater than 30.6% cover of other species had the greatest abundance. Within plots with low vegetation cover, those with lower nitrate availability had the greatest *Carex* abundance (9.56%), while for plots with higher vegetation cover aboveground standing crop was important with the greatest *Carex* cover (15.8% vs. 8.45%) in plots with less than 55.4 g/m^2 aboveground standing crop.

Far from talus, soil depth was most important at predicting *Carex* abundance, but nitrate availability was also identified (Fig. 3-3d). Plots with deeper soil than 12.3 cm had higher *Carex* cover (5.14% vs. 15.12%). Within these plots with deep soil, those with high nitrate availability (> 3.54ppm) had higher abundance, while for plots with lower nitrate those with soil deeper than 23.5 cm had the greatest *Carex* cover.

DISCUSSION

Controls on interaction strength & direction

Nutrients were related to competitive response for both species and were especially important near to talus, although the direction of the relationship was not always consistent (Fig. 3-2). For *Artemisia*, nitrate availability was associated with competitive response at both distances, while for *Carex* ammonium availability was important (Fig. 3-2). A number of studies have shown that species are better able to absorb one of the two forms of inorganic nitrogen (Falkengren-Gerup, 1995; Turnbull *et al*, 1996). Specifically in alpine systems, *Artemisia scopulorum* has been shown to preferentially absorb nitrate ions, while *Carex rupestris* shows preference for ammonium ions (Miller & Bowman, 2002).

The relationship between competitive response and nutrient availability was different from expected. We expected that as these nutrients increased in the soil, that competition for them would become less intense (Wilson & Tilman, 1993; Casper & Jackson, 1997; Cahill, 1999). While this is the case for *Carex* far from talus, for all of the other species-distance combinations, facilitation was present with low nutrient availability and competition with high nutrient availability. It is likely that both above- and belowground productivity increases with nutrient availability in this system, therefore competition could be more intense in those areas with high productivity (Campbell & Grime, 1992; Goldberg & Barton, 1992). At low nitrogen availability neighbours may also increase nutrient levels through nitrogen rich litter decomposition (Siemann & Rogers, 1993; Steltzer & Bowman, 1998), which may result in facilitation.

Soil depth was important for *Artemisia* far from talus. Plots with soil depths between ~ 14 and 19 cm showed strong competition, while on either side there was weak competition or facilitation. Soil fertility usually increases with soil depth (Belcher *et al*, 1995). Therefore it could be that at shallow depths nutrients were present at low concentration, which resulted in low plant productivity and weak competition. Deeper soils with more nutrients would have greater productivity and competition (Reader & Best, 1989; Campbell & Grime, 1992; Gerdol, 2000). It is unclear why there is facilitation with deeper soil. Increased plant standing crop at higher soil fertility could mean that neighbours are better able to provide shelter to neighbouring plants, both from harsh climatic conditions and herbivores. At lower standing crop these facilitative mechanisms will be weak and may not contribute significantly to plant growth.

At both distances for *Carex,* the amount of aboveground standing crop was related to competitive response. Yet for both distances competition was more intense when standing crop values were small, with weak competition or facilitation present with higher standing crop values. Aboveground competition has been seen to be positively related to biomass (Reader & Best, 1989; Bonser & Reader, 1995; Choler *et al*, 2001) or independent (Reader *et al*, 1994; Wilson & Tilman, 1993), but rarely if ever negative. Aboveground competition for light is assumed to be of minor importance in this system because of the low stature of the vegetation. Plots with low aboveground biomass therefore may have had significantly more belowground competition, which could account for the negative relationship between biomass and competition strength (Tilman, 1985; Wilson & Tilman, 1991). Above- and belowground competition were not separated and belowground measures of biomass were not taken during this study so this

remains an open question. These results may also be due to the mechanism of facilitation requiring higher plant biomass to be effective, as mentioned previously.

Far from talus, grazing was also important for *Carex*. Plots where no plants were grazed had stronger competition than those where grazing occurred. This is what might be expected, since grazing can decrease plant biomass and reduce the ability of plants to sequester resources and prevent access to them by their neighbours (Olofsson *et al*, 2002; van der Wal *et al*, 2000). Grazing could also stimulate regrowth (Paige, 1987 &1999), which might increase competition for resources. However, plants far from talus did not show as great an increase in leaf births when grazed as plants near to talus (Chapter 2). It is surprising that herbivory is only important for one species-distance combination, as *Artemisia* is also preferred forage and experienced high grazing pressure near to talus.

Near to talus, snowmelt was the final variable important for *Carex* competitive response. Snowmelt has been shown to be important in alpine areas with respect to growing season length, species distributions, nutrient availability and soil moisture (Korner, 2003). In this study, plots with earlier snowmelt had stronger competition, which could be due to growing season length. With more time to grow plants in these plots can draw down resources to a greater degree and increase the intensity of competition. Competition intensity has been previously reported to be lower in alpine areas with late snowmelt (Kudo & Ito, 1992).

Many studies have shown that facilitative interactions between plants become more important as stress increases, specifically in alpine systems (Choler *et al*, 2001; Callaway *et al*, 2002). This is interpreted as evidence that as stress increases plants are less able to compete for resources while simultaneously, shelter by neighbours from the harsh

climatic conditions becomes more important. While this can be true over large-scale gradients such as elevation, significant variation can be present within this gradient. Our results suggest over small spatial scales that the relationship between stress and competition strength is not as clear. Even at low resource levels that could be considered "stressful", competition can still be intense. Facilitation can also be present, even as levels of stress decrease and plants have more access to nutrients.

This study suggests that combinations of abiotic and biotic factors can significantly affect the strength and direction of plant interactions over short spatial scales. It is accepted that species distributions and abundances can be determined by these factors, but relationships with competition strength have rarely been investigated. It is also generally accepted that plant interactions, specifically competition, are extremely important in determining the structure of communities and species distributions. Therefore the synthesis of these two knowledge sets should be important for advancing models of how species interact with each other and how this translates into community structure and composition. This has rarely been done and should be a subject for further study in numerous systems.

Species abundance

The variables associated with species abundance were much different than those related to competitive response for both species at both distances. Near to talus, plant cover was the most important variable for both species. Plots with higher cover had greater *Artemisia* or *Carex* abundance than those with lower cover. Plant cover may be a good metric of the long-term conditions present in an area; those with high plant cover

can indicate favourable conditions for plant growth. The importance of cover may be also related to the amount of suitable substrate available near to talus for plant growth. Close to talus there were more areas of bare rock where plants cannot grow.

Interestingly, nitrate availability was related to *Carex* abundance while ammonium availability was important for predicting competitive response for *Carex*. Near to talus plots with lower nitrate availability had greater *Carex* abundance, while far from talus this relationship was reversed. This may be related to species composition differences between the two distance to talus and subsequent effects on nitrate availability and competition intensity. Nitrate ions are rapidly taken up from alpine soils by plants, with each species having a different ability to deplete nitrate from the soil. Differences in species composition between distances could have significant impacts on nutrient availability and subsequent species distribution.

Conclusions

The variables important in predicting competitive response for both species were in most cases completely different for species abundance. Additionally, in only one case (*Artemisia* near to talus) was the competitive response experienced by that species related to its abundance. There are a number of possible reasons for these differences. We calculated competitive response using aboveground biomass measures, and this might not be a good measure of plant fitness in this system. The clonal nature of the plants could make underground organs much more important to the future success and reproductive effort of these plants. Unfortunately it was not feasible to collect underground parts of

these plants and we cannot make any conclusions about the impacts of neighbours on belowground growth.

Alternatively, the direction and intensity of competition over short time periods might not be important over the long-term in determining species abundance. Interactions between plants could be important in the growth of a plant over a single growing season but fluctuations in abiotic conditions and climate could significantly change competitive interactions and their consequences over time (Herben *et al*, 2003; Heegaard, 2004). Therefore, the outcome of plant interactions measured over one or two growing seasons will probably not be a good measure of long-term trends and the important controls on plant population dynamics in these systems.

Weldon & Slauson (1986) make the distinction between the importance and intensity of plant interactions. While competition or facilitation can be intense, this does not mean that they will be important for the fitness of individual plants relative to other factors. In fact, there is no overlying reason why the importance and intensity of these interactions should be correlated (Weldon & Slauson, 1986).

While this study focused on the strength and direction of interaction outcomes for two focal species this may not be a useful approach. Neither competition nor facilitation appear to be driving species abundances in this system. Identification of the factors that actually determine community patterns will be more useful to our understanding of how this and other systems function and for predicting future changes or trends.

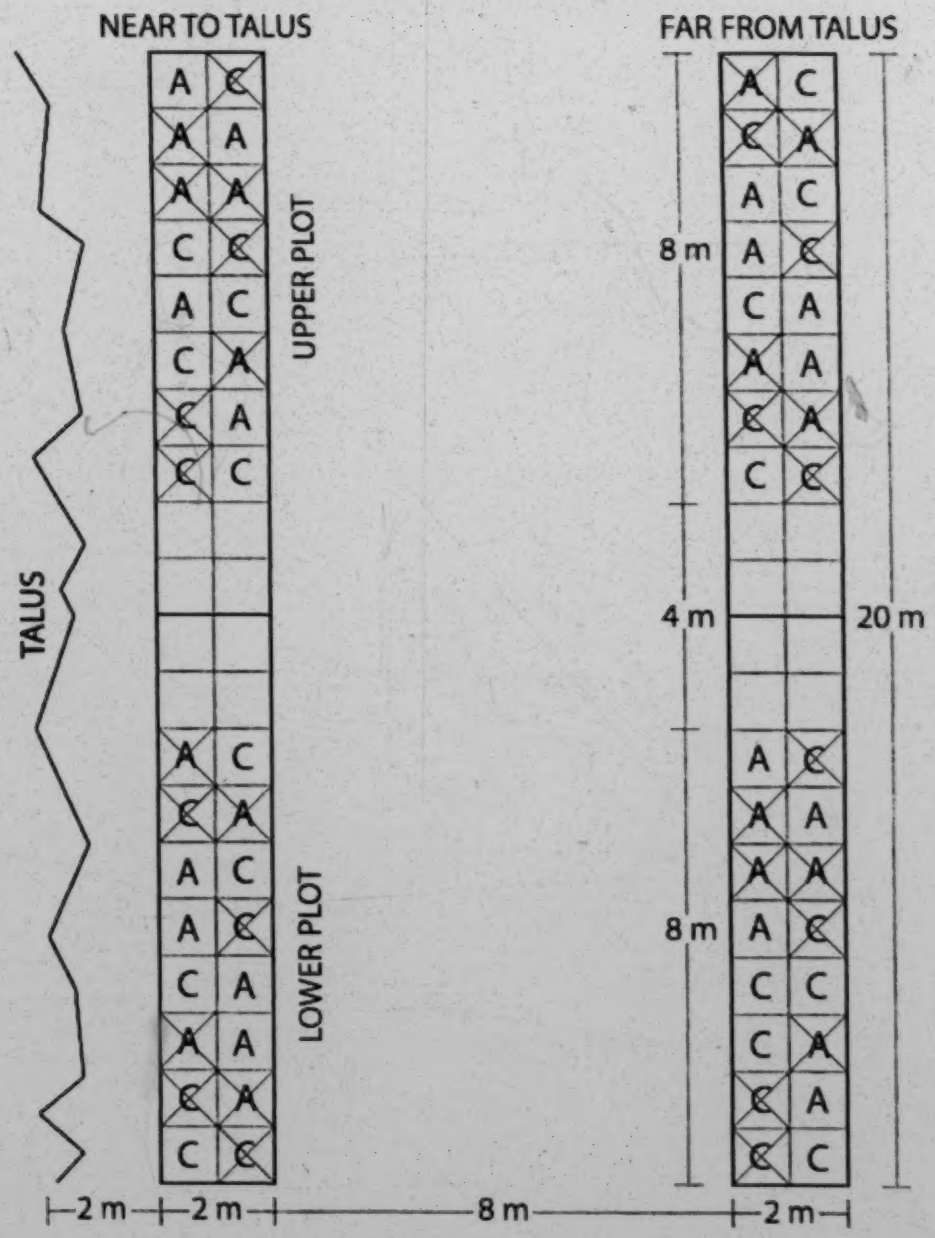

Fig. 3-1 – Schematic of an experimental block containing two plots near to talus and two far from talus. *Artemisia norvegica* individuals are represented by A's, *Carex consimilis* individuals by C's. Individuals that have had all neighbours removed are inside crossed out boxes. The near plot (+ Herbivory) is within 2m of the talus margin, the far plot (- Herbivory) is located 8m from the near plot.

Table 3-1 – Values of abiotic and biotic variables near to talus and far from talus. The first 8 variables were used in creating regression trees on competition response and species abundance for *Artemisia norvegica* and *Carex consimilis*. *F* and *P* values for the differences between distances are from general linear mixed effects models. Degrees of freedom are in parentheses with the *F*-values.

Variable	Near To Talus		Far From Talus		$F_{(d.f.)}$	*P*
	Mean	S.D.	Mean	S.D.		
Aboveground Standing Crop	64.35 g/m^2	0.422	63.68 g/m^2	0.458	$0.01_{(1,5.3)}$	0.946
Plant Cover	38.57%	2.185	41.20%	2.370	$0.55_{(1,9.0)}$	0.476
Soil Depth	13.15 cm	0.895	17.89 cm	1.458	$6.55_{(1,11.8)}$	**0.025**
Nitrate Availability	0.98 ppm	0.050	2.67 ppm	0.342	$18.94_{(1,11.1)}$	**0.001**
Ammonium Availability	2.14 ppm	0.164	2.49 ppm	0.298	$0.88_{(1,12.0)}$	0.367
Snowmelt Date	May 17th	1.518	May 11th	0.764	$10.44_{(1,14.0)}$	**0.006**
Artemisia Herbivory Level	41.30%	5.121	21.73%	3.828	$9.76_{(1,7.0)}$	**0.017**
Carex Herbivory Level	19.17%	3.223	21.02%	2.684	$0.24_{(1,6.3)}$	0.643
Alpha Diversity*	20.7	4.440	20.8	4.930	$0.07_{(1,14.0)}$	0.796
Beta Diversity§	3.7	n/a	3.4	n/a	n/a	n/a
Gamma Diversity†	76	n/a	71	n/a	n/a	n/a

* average number of species per plot; species richness

§ amount of compositional change within the set of sample units (gamma diversity ÷ alpha diversity)

† total number of species

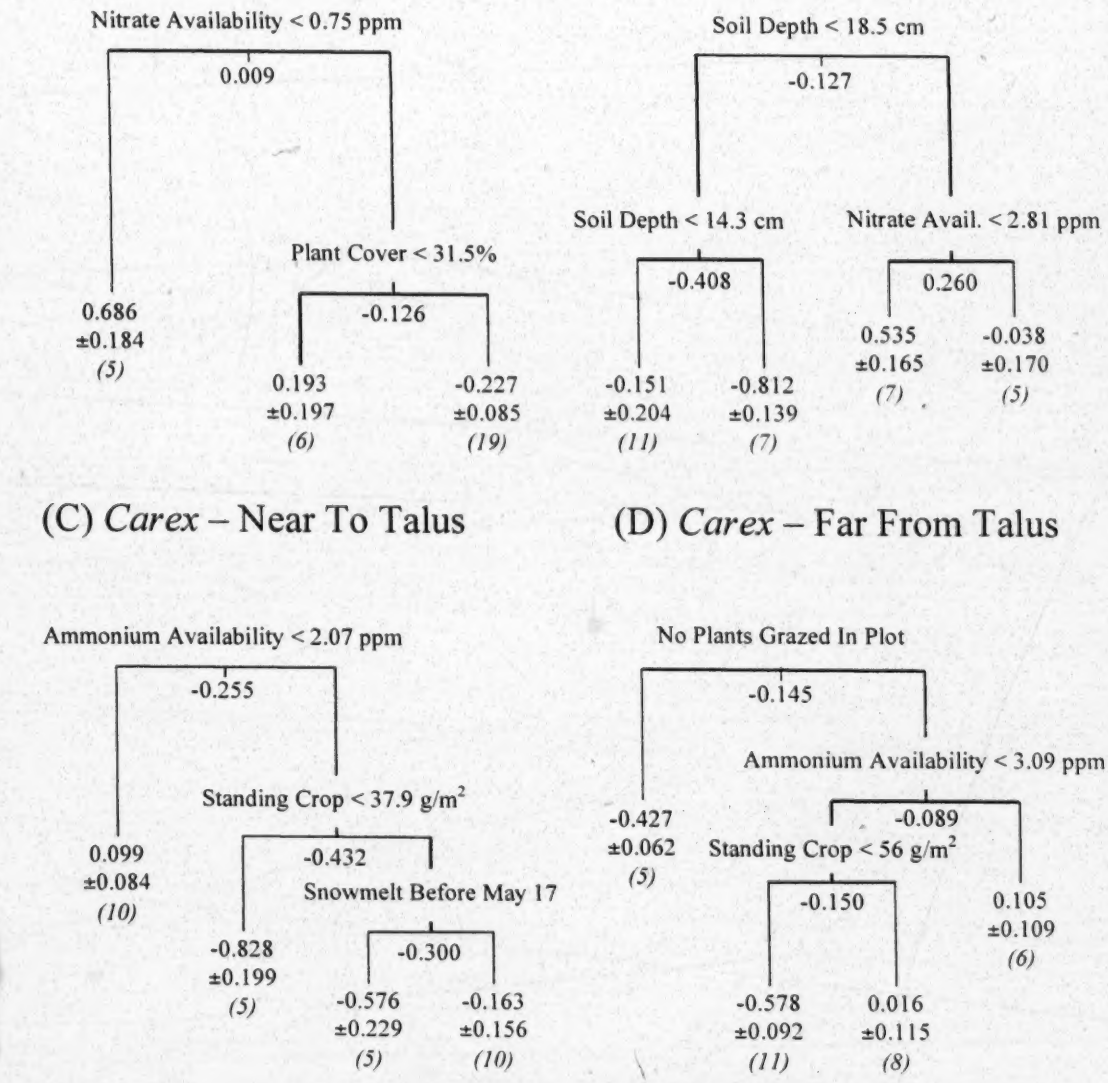

Fig. 3-2 – Regression trees for the competition response (log response ratio calculated from aboveground plant biomass ± 1SE) experienced by *Artemisia norvegica* and *Carex consimilis* near to talus and far from talus. Branches to the left of the splits are those that agree with the splitting criteria and branch lengths represent the relative amount of deviance explained by the split. Values at the end of branches are average values of competition response for plots within that group while values within parentheses represent the number of plots for that group. Deviance explained is 45.1% in (a), 47.3% in (b), 42.8% in (c) and 35.3% in (d).

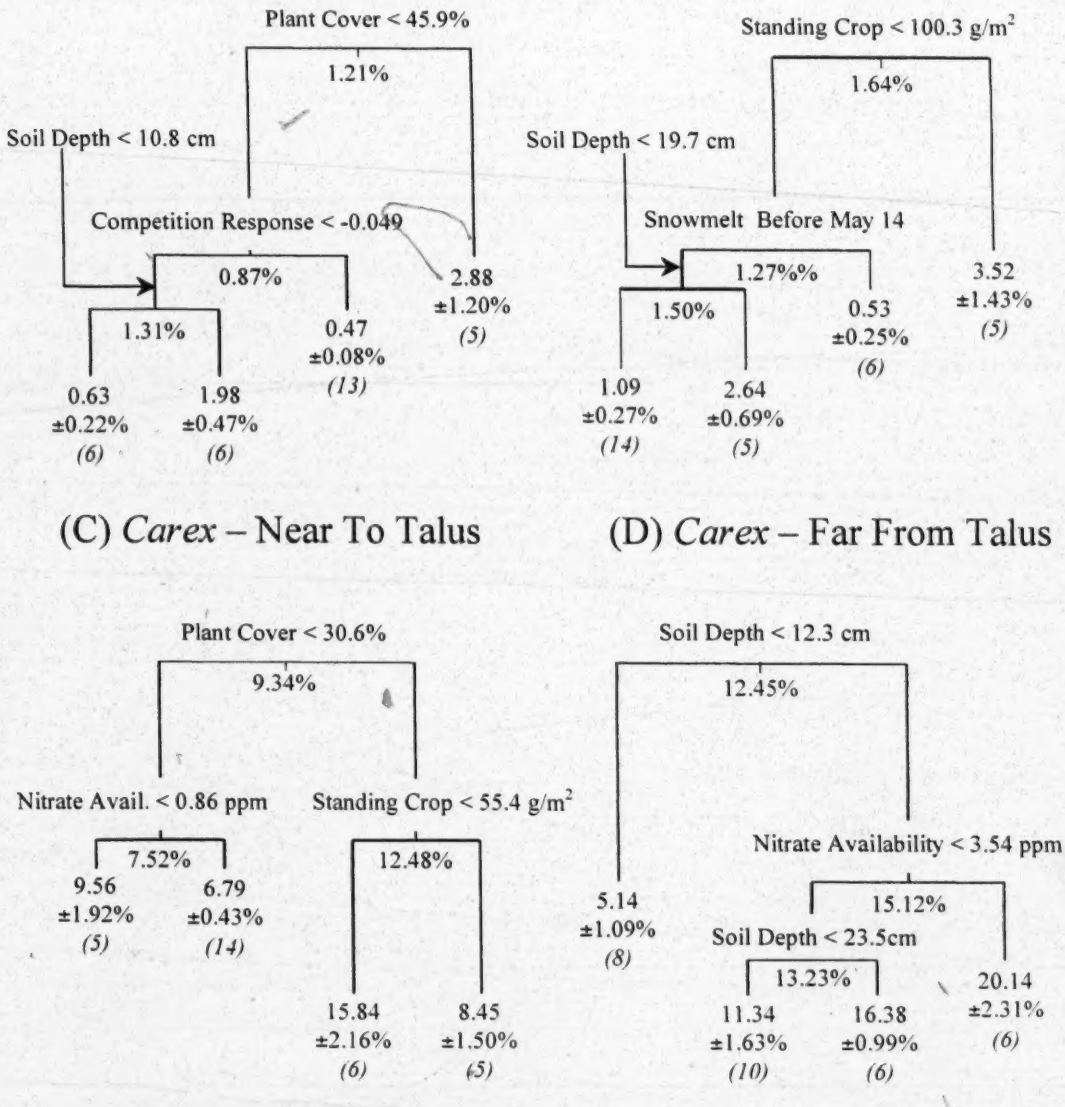

Fig. 3-3 – Regression trees for the species abundance (% cover) of *Artemisia norvegica* and *Carex consimilis* near to talus and far from talus ± 1SE. Branches to the left of the splits are those that agree with the splitting criteria and branch lengths represent the relative amount of deviance explained by the split. Values at the ends of branches are average values of species abundance for plots within that group while values within parentheses represent the number of plots for that group. Deviance explained is 41.2% in (a), 34.9% in (b), 54.3% in (c) and 64.1% in (d).

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CHAPTER 4

GENERAL DISCUSSION

This thesis reported on the outcome of plant interactions in a subarctic-alpine system over two growing seasons with respect to experimental treatments of precipitation and grazing pressure, and also underlying local-scale abiotic and biotic factors. Responses were recorded as changes in leaf births and deaths as well as aboveground biomass at the end of the study. Other studies have investigated the outcome of plant interactions in a variety of systems, including arctic and alpine areas, but few have identified the effect of specific local-scale factors that influence the outcome of plant interactions.

A main result from my experiment was that although the overall outcome of plant interactions in this system appeared to be weakly competitive, there are simultaneously both competitive and facilitative interactions at work. This adds to the accumulating evidence that simultaneous competitive and facilitative interactions between plants are the norm in most systems. Additionally, the balance between these interactions can be altered by specific local scale environmental factors, which can have a greater influence on species distributions and abundances than the specific plant-plant interactions that are present. While the intensity of interactions between neighbouring plants in this system can be high, as measured by reductions in soil nutrients, the importance of such interactions can be minor when compared to the overlying abiotic conditions. The specific relationships between local scale factors and plant interactions have rarely been investigated, but identifying these relationships will help improve the predictive ability of

community ecology (Kikvidze *et al*, 2005). I have identified these processes for only two species in this system, *Artemisia norvegica* and *Carex consimilis*, therefore the implications for overall community and population dynamics in this system are still unresolved.

The balance between competition and facilitation

Most studies, including this one, measure the overall outcome of plant interactions on some measure of plant growth or fitness. While this is often easiest, important processes such as facilitation can be masked by strong competition (Brooker & Callaghan, 1998; Olofsson *et al*, 1999; Pugnaire & Luque, 2001; Bruno *et al*, 2003). It is now accepted that complex combinations of competition and facilitation are widespread and are present in a variety of systems (Callaway, 1995; Callaway & Walker, 1997; Kikvidze *et al*, 2005), and that the balance between the two can depend on abiotic stress, consumer pressure, plant life stage, and plant size (Callaway & Walker, 1997). In this study, both competition and facilitation occurred, but through very different mechanisms. Competition was for belowground soil nitrate while facilitation occurred through neighbouring plants reducing the grazing pressure on focal plants (Chapter 2). Plants that had close neighbours were less visually apparent to herbivores and were not as heavily grazed. This outcome supports the prediction that in harsh environments, where positive interactions can be increasingly important, plants can both improve and worsen the abiotic environment around them (Olofsson *et al*, 1999; Kikvidze *et al*, 2005).

My results show that competition can be intense, even in systems where plant productivity is low. While I did not specifically investigate interaction outcomes along a

productivity gradient, my results give some support to the theory that competition strength is independent of productivity (Tilman, 1990; Taylor *et al*, 1990). Instead, the resources in question shift from aboveground to belowground as productivity decreases. Competition in this system was primarily underground, and overall competition for these resources decreased plant size and growth. While plants in unproductive environments may be unable to deplete resources to the degree of plants in more productive systems, resources are already at such low levels that competition for them can still be quite intense. What can be more relevant, and may explain why competition appears to be less intense in these systems, is a simultaneous increase in the strength of facilitative interactions as stress increases and plant productivity decreases (Pugnaire & Luque, 2001). In this system, the relatively strong competitive interactions for soil nutrients appear to be balanced by the ability of neighbours to reduce consumer pressure, thereby causing the overall outcome to be weakly competitive.

I was able to identify these simultaneous processes because I used both aboveground biomass at the end of the experiment as well as leaf demography variables over the entire course of the study. It is unlikely that the presence of facilitation would have been identified if only biomass measures had been used. This outcome emphasizes the need for multiple measures of plant performance and how the outcomes of plant interactions may not tell the entire story of how plants interact with each other.

It also became apparent through the leaf demography data that the balance between competition and facilitation was dependent on abiotic variables as well as plant characteristics such as plant size. While experiments that include multiple factors and their interactions can be difficult to interpret, they significantly increase the realism and

applicability of an experiment to natural systems and processes and are extremely important where ecological processes are not discrete (Haag *et al*, 2004). As stated by Callaway and Walker (1997): "Interactions among organisms take place within a complex milieu of abiotic and biotic processes, but we generally study them as solitary phenomenon." If we want to increase our understanding of how species interact it will be necessary to use more complicated experimental designs. Future studies, whether in the field or the greenhouse, should attempt to include multiple treatments in a factorial way. In particular, the effects of abiotic conditions such as climate and soil nutrients as well as different life stages and specific genotypes of plant species should be included. The possibility of complex interactions should not deter us from using these designs if they will help advance our knowledge of interactions in natural systems and the predictive power of our ecological models.

Complicated interactions

Leaf births and deaths for *Artemisia* individuals were determined by complicated interactions between grazing history, watering, neighbour presence, current season grazing status, and plant size. These results are not unexpected, plant growth should be determined by numerous abiotic and biotic factors and not just a single variable. The consequence of these results for future experiments on plant growth and interactions in this system is that these variables must be taken into account either in the experimental design used or the interpretation of the results. This will add substantial complexity to future experiments but will also improve the ability to model and predict future changes and patterns in plant growth and interactions.

Plant interactions at multiple scales

My results also highlight the fact that different outcomes of plant interactions become apparent at different spatial scales. Over the entire study, the overall outcome of plant interactions was competitive. At a finer scale both competition and facilitation become evident (Chapter 3). Alpine systems have large variation in microclimate and environmental variables (Korner, 2002). Over very short distances there can be large changes in the prevailing climate, snow depth, soil nutrients, soil moisture, and specifically in this ecosystem, grazing pressure. My results show that changes in these variables can have significant effects on the outcome of plant interactions. Additionally, there is evidence that species identity and the morphological and physiological characteristics of each species can affect which of the abiotic variables is important. Along large-scale stress gradients in alpine systems it has been shown that generally there is a shift from competition to facilitation that may determine the boundaries of species distributions (Choler *et al*, 2001; Callaway *et al*, 2002). However, my results suggest that significant variation in interaction strength and direction could be present within this gradient that will be important for local-scale species distributions and composition.

The strength and direction of these interactions appear to have little or no relationship with the abundance of either focal species. In other words, the importance of plant interactions does not appear to be correlated with the intensity of these interactions in this system (Weldon & Slauson, 1986). It is often assumed that plant interactions will directly influence the fitness of specific individuals and species, therefore controlling population dynamics, species abundance, and community structure. This may be true in

systems where abiotic conditions are more conducive for plant growth and the relative importance of competition for plant growth is high. In systems where abiotic conditions are harsh and resources are in short supply, plant interactions may only be important for plant growth over short periods of time, for example within growing seasons. Over the long-term, overlying environmental conditions such as snowfall, temperature, and extreme climate events will probably have a much larger influence in determining species distributions and abundances (Weldon & Slauson, 1986).

Future Study

This system provides an ideal place to test the effects of long-term grazing history on species composition, plant growth, and nutrient cycling, and a number of studies have been performed in this system, which include this factor (McIntire 1999; McIntire & Hik 2002, 2005; Tait, 2002). My results show that there are significant differences in species composition between areas with different grazing histories. However, these differences in grazing history are confounded by differences in soil resources, soil depth and snowmelt along the distance from talus gradient. Further work is needed to separate the effects of these underlying abiotic factors from any long-term plant adjustments or population level changes that historical grazing levels can cause. In particular, the relative importance of the various abiotic and biotic variables along this distance from talus gradient should provide valuable information about the long-term consequences and interactions of these processes on plant fitness.

I was not able to observe the effects of my experimental treatments or the underlying abiotic conditions on belowground biomass allocation in these species. It

became apparent that underground interactions between plants were important, but underground roots were not collected because it is so difficult to do in these environments. It is known that changes in abiotic variables and productivity can cause shifts in the interactions between root and shoot competition, and that measures of aboveground competition will not provide reliable information about the strength of belowground competition when such interactions are present (Cahill 1999 & 2002). Any future work should therefore attempt to determine the belowground dynamics in this system as they may provide more information about plant interactions than aboveground processes alone.

Alpine and arctic systems are predicted to undergo rapid climate change in the near future, including increased temperatures, snowfall, and precipitation as well as increased variability in climate (ACIA, 2004). My study system in particular is in an area that is predicted to experience large increases in temperature and precipitation (ACIA, 2004). My results suggest that changes in growing season precipitation will have only subtle effects on plant growth and interactions if any, and only in combination with herbivory. Combining other climate change factors such as increased temperatures and greater soil nutrients from increased plant litter deposition with herbivory and increased precipitation will help us understand the long-term consequences of these changes on alpine and arctic systems. My results highlight that grazing is an important variable in determining plant growth and species composition in this system and should be included in any future studies on long-term dynamics of alpine meadow communities.

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APPENDIX

MIXED MODEL ANCOVA RESULTS: LEAF BIRTHS & DEATHS

Table A-1 – General linear mixed models of the effects of distance from talus, watering, neighbour removal, grazing status and initial plant size (# live leaves) on leaf births and leaf deaths for *Artemisia norvegica* and *Carex consimilis* individuals. Bold values indicate significance at $P < 0.05$; degrees of freedom were calculated using Satterthwaite's method.

Level	*Artemisia norvegica*				*Carex consimilis*			
	Leaf Births		Leaf Deaths		Leaf Births		Leaf Deaths	
	$F_{(numdf,dendf)}$	*P*-value	$F_{(numdf,dendf)}$	*P*-value	$F_{(numdf,dendf)}$	*P*-value	$F_{(numdf,dendf)}$	*P*-value
Distance	$0.29_{(1,436)}$	0.5885	**$6.99_{(1,437)}$**	**0.0085**	$0.90_{(1,372)}$	0.3438	$0.40_{(1,334)}$	0.5284
Water	$2.99_{(1,443)}$	0.0844	$1.92_{(1,429)}$	0.1671	$3.08_{(1,360)}$	0.0800	$1.19_{(1,350)}$	0.2763
Distance x Water	$0.01_{(1,445)}$	0.9343	$0.22_{(1,432)}$	0.6419	$0.11_{(1,357)}$	0.7426	$0.19_{(1,357)}$	0.6612
Neighbour Removal	$2.46_{(1,433)}$	0.1172	$0.04_{(1,415)}$	0.8468	**$8.94_{(1,376)}$**	**0.0030**	$0.00_{(1,383)}$	0.9552
Distance x Neighbours	$1.05_{(1,429)}$	0.3067	$0.09_{(1,419)}$	0.7683	$1.18_{(1,379)}$	0.2775	$0.82_{(1,383)}$	0.3650
Water x Neighbours	$0.02_{(1,442)}$	0.8999	$0.40_{(1,431)}$	0.5251	$0.29_{(1,366)}$	0.5900	$1.42_{(1,383)}$	0.2339
Dist x Water x Neigh	$0.16_{(1,438)}$	0.6927	$3.64_{(1,431)}$	0.0570	$0.02_{(1,355)}$	0.8812	$0.04_{(1,383)}$	0.8458
Grazing	$1.55_{(1,440)}$	0.2139	$0.12_{(1,435)}$	0.7338	$0.14_{(1,378)}$	0.7132	$0.21_{(1,380)}$	0.6433
Distance x Grazing	$0.53_{(1,442)}$	0.4667	$8.52_{(1,413)}$	0.0037	$0.41_{(1,379)}$	0.5246	$0.38_{(1,380)}$	0.5391
Water x Grazing	$1.74_{(1,437)}$	0.1876	$1.57_{(1,422)}$	0.2110	$0.88_{(1,365)}$	0.3493	$0.41_{(1,377)}$	0.5224
Dist x Water x Grazing	$2.23_{(1,439)}$	0.1360	$0.31_{(1,427)}$	0.5810	$0.03_{(1,353)}$	0.8643	$0.30_{(1,378)}$	0.5849
Neighbours x Grazing	$1.33_{(1,439)}$	0.2486	$0.02_{(1,432)}$	0.8853	$1.76_{(1,374)}$	0.1854	$0.04_{(1,382)}$	0.8431
Dist x Neigh x Graz	$0.37_{(1,437)}$	0.5439	$2.48_{(1,433)}$	0.1160	$0.05_{(1,378)}$	0.8187	$1.26_{(1,383)}$	0.2630
Water x Neigh x Graz	$0.60_{(1,438)}$	0.4388	$0.17_{(1,430)}$	0.6817	$1.91_{(1,368)}$	0.1674	$0.87_{(1,384)}$	0.3520
Dist x Wat x Neig x Gra	**$3.99_{(1,433)}$**	**0.0463**	**$5.71_{(1,429)}$**	**0.0173**	$0.44_{(1,356)}$	0.5083	$0.60_{(1,383)}$	0.4405
Size	**$20.79_{(1,387)}$**	**<0.0001**	**$29.85_{(1,347)}$**	**<0.0001**	$2.10_{(1,371)}$	0.1485	$0.07_{(1,363)}$	0.7917
Size x Distance	$0.21_{(1,389)}$	0.6462	**$6.79_{(1,437)}$**	**0.0095**	$0.56_{(1,375)}$	0.4564	$0.27_{(1,345)}$	0.6034
Size x Water	**$3.89_{(1,442)}$**	**0.0492**	$2.44_{(1,420)}$	0.1193	$3.65_{(1,359)}$	0.0567	$1.78_{(1,360)}$	0.1824
Size x Distance x Water	$0.03_{(1,444)}$	0.8726	$0.53_{(1,430)}$	0.4686	$0.01_{(1,345)}$	0.9128	$0.00_{(1,364)}$	0.9579
Size x Neighbours	$0.08_{(1,384)}$	0.7780	$0.00_{(1,426)}$	0.9677	**$6.16_{(1,367)}$**	**0.0135**	$0.00_{(1,383)}$	0.9785

Level	*Artemisia norvegica*				*Carex consimilis*			
	Leaf Births		Leaf Deaths		Leaf Births		Leaf Deaths	
	$F_{(numdf,dendf)}$	*P*-value	$F_{(numdf,dendf)}$	*P*-value	$F_{(numdf,dendf)}$	*P*-value	$F_{(numdf,dendf)}$	*P*-value
Size x Distance x Neigh	$1.35_{(1,382)}$	0.2461	$0.13_{(1,432)}$	0.7184	$0.27_{(1,376)}$	0.6036	$0.80_{(1,383)}$	0.3724
Size x Water x Neigh	$0.20_{(1,440)}$	0.6538	$0.31_{(1,432)}$	0.5757	$0.45_{(1,364)}$	0.5037	$1.62_{(1,383)}$	0.2041
Size x Dist x Wat x Neig	$0.01_{(1,439)}$	0.939	$3.79_{(1,432)}$	0.0522	$0.12_{(1,340)}$	0.7246	$0.13_{(1,383)}$	0.7147
Size x Grazing	**$9.04_{(1,442)}$**	**0.0028**	$2.12_{(1,340)}$	0.1466	$0.57_{(1,371)}$	0.4516	$0.24_{(1,380)}$	0.6244
Size x Dist x Grazing	$1.63_{(1,445)}$	0.2018	**$7.13_{(1,406)}$**	**0.0079**	$0.38_{(1,377)}$	0.5396	$0.20_{(1,379)}$	0.6537
Size x Water x Grazing	$2.46_{(1,443)}$	0.1177	$1.60_{(1,407)}$	0.2064	$1.27_{(1,363)}$	0.2600	$0.54_{(1,376)}$	0.4634
Size x Dist x Wat x Gra	$3.40_{(1,444)}$	0.0659	$0.15_{(1,425)}$	0.6968	$0.01_{(1,338)}$	0.9365	$0.14_{(1,378)}$	0.7097
Size x Neigh x Graz	$0.90_{(1,440)}$	0.3434	$0.01_{(1,427)}$	0.9350	$2.19_{(1,365)}$	0.1395	$0.01_{(1,381)}$	0.9052
Size x Dist x Neig x Gra	$0.81_{(1,440)}$	0.3701	$3.05_{(1,428)}$	0.0813	$0.16_{(1,376)}$	0.6928	$1.10_{(1,383)}$	0.2957
Size x Water x Nei x Gra	$0.33_{(1,443)}$	0.5633	$0.29_{(1,426)}$	0.5936	$2.36_{(1,366)}$	0.1252	$1.05_{(1,384)}$	0.3063
S x D x W x N x G	$3.83_{(1,439)}$	0.0511	**$5.27_{(1,427)}$**	**0.0222**	$0.61_{(1,341)}$	0.4353	$0.32_{(1,384)}$	0.5728